IOWA STATE UNIVERSITY LIBRARY

JOURNAL OF THE FISHERIES RESEARCH BOARD OF CANADA

Volume 21, No. 5

CONTENTS

	Pages
Editor's Foreword	(i)
W. A. Clemens—An appreciation. By W. S. Hoar	869–872
Pareen, R. R., and L. Margolis. A new species of parasitic copepod, *Caligus clemensi* sp. nov. (Caligoida: Caligidae), from pelagic fishes in the coastal waters of British Columbia	873–889
Manzer, J. I. Preliminary observations on the vertical distribution of Pacific salmon (genus *Oncorhynchus*) in the Gulf of Alaska	891–903
Ricker, W. E. Ocean growth and mortality of pink and chum salmon	905–931
Rosenblatt, Richard H. A new gunnel, *Pholis clemensi*, from the coast of western North America	933–939
Tully, John P. Oceanographic regions and assessment of temperature structure in the seasonal zone of the north Pacific Ocean	941–970
Bowles, T. H. Redescription of the parasitic isopod *Haliophyxus alaskensis* Richardson, and a note on its synonymy	971–976
Limbaby, C. C. Problems in zoogeography of the lake trout, *Salvelinus namaycush*	977–994
McInerney, John E. Salinity preference: an orientation mechanism in salmon migration	995–1018
Parker, Robert R. Estimation of sea mortality rates for the 1960 brood-year pink salmon of Hook Nose Creek, British Columbia	1019–1034
Idler, D. R., T. Tamura and T. Wainai. Seasonal variations in the sterol, fat and unsaponifiable components of scallop muscle	1035–1042
Scott, D. P. Thermal resistance of pike (*Esox lucius* L.), muskellunge (*E. masquinongy* Mitchill), and their F_1 hybrid	1043–1049
Ketchen, K. S. Preliminary results of studies on growth and mortality of Pacific cod (*Gadus macrocephalus*) in Hecate Strait, British Columbia	1051–1067
Northcote, T. G., Mildred S. Wilson and D. R. Hoar. Some characteristics of Nitinat Lake, an inlet on Vancouver Island, British Columbia	1069–1081
Fujiwara, Wolfgang, and T. F. Fletcher. Club cells and granular cells in the skin of lamprey	1083–1088
Muntz, J. A. C. Reflectivity of the choroidal tapeta of selachians	1089–1100

(*Continued overleaf*)

OTTAWA

SEPTEMBER

1964

LeBrasseur, R. J., and R. R. Parker. Growth rate of central British Columbia pink salmon (*Oncorhynchus gorbuscha*) 1101–1128
Hubbs, Carl L., and Norman J. Wilimovsky. Distribution and synonymy in the Pacific Ocean, and variation, of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum) 1129–1154
Quayle, D. B. Distribution of introduced marine Mollusca in British Columbia waters 1155–1181
Brett, J. R. The respiratory metabolism and swimming performance of young sockeye salmon 1183–1226
Neave, Ferris. Ocean migrations of Pacific salmon 1227–1244
Larkin, P. A., and A. S. Hourston. A model for simulation of the population biology of Pacific salmon 1245–1265
Belton, H. T., D. W. Jenkinson and M. P. Shepard. A key to five species of Pacific salmon (genus *Oncorhynchus*) based on scale characters 1267–1288
Waldichuk, Michael. Dispersion of kraft-mill effluent from a submarine diffuser in Stuart Channel, British Columbia 1289–1316

NOTES

A quantitative estimate of the number of Pacific herring in a spawning population. By D. N. Outram and F. H. C. Taylor 1317–1320
Occurrence and distribution of sea water in Sakinaw Lake, British Columbia. By T. G. Northcote and W. E. Johnson 1321–1324
Successful introduction of *Mysis relicta* Lovén into Kootenay Lake, British Columbia. By R. A. H. Sparrow, P. A. Larkin and R. A. Rutherglen 1325–1327
Further information on spawning stock size and resultant production for Skeena sockeye. By M. P. Shepard, F. C. Withler, J. McDonald and K. V. Aro 1329–1331
Contribution to the marine life history of the eulachon *Thaleichthys pacificus*. By W. E. Barraclough 1333–1337
Distinguishing characters for the sculpins *Cottus bairdii* and *C. cognatus* in eastern Canada. By D. E. McAllister 1339–1342

Recent articles 1343–1344

Editor:
J. C. Stevenson

Associate Editor:
E. G. Bligh

Fisheries Research Board of Canada
Sir Charles Tupper Building
Ottawa, Ont., Canada

Manuscripts for publication should be addressed to the Editor

ROGER DUHAMEL, F.R.S.C.
QUEEN'S PRINTER AND CONTROLLER OF STATIONERY
OTTAWA, 1964

EDITOR'S FOREWORD

This special issue of the Journal of the Fisheries Research Board of Canada was planned in early 1964 to honour Dr W. A. Clemens for his outstanding contribution to fisheries research.

On June 21, 1964, when this issue was in press, Dr Clemens passed away in Vancouver.

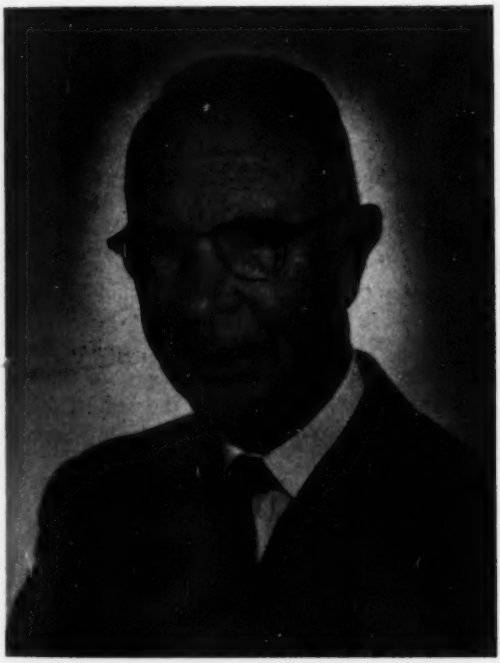
To the memory of this eminent and well-beloved Canadian scientist, this volume is dedicated.

Ottawa, August 1, 1964

J. C. STEVENSON

W. A. CLEMENS — An Appreciation

Just 40 years ago, W. A. Clemens left his professorial post in the University of Toronto to become the first year-round Director of the Pacific Biological Station of the Biological Board of Canada (now the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.). There he met the challenge of mustering its first permanent scientific staff and shaped the first program of fisheries research on the Canadian Pacific coast. A host of biologists came under his influence either at Toronto in the early twenties, at the Pacific Biological Station for a period of 16 years, or at the University of British Columbia for almost a quarter of a century thereafter. Today, they pay tribute to him as teacher, scientist, and man.



Born in Millbank, Ontario, in 1887, he started his professional career as a public school teacher in Haysville at the age of 18. This experience was to his liking and he embarked on University training in 1908 with the ultimate goal of teaching in the high schools of Ontario. Although he subsequently taught in the rural schools of Saskatchewan for three summers to finance his University studies, the plan to teach high school never materialized. Instead, he came under the influence of Toronto's great pioneer zoologists—Professors R. Ramsay Wright, B. A. Bensley, W. H. Piersoll, E. M. Walker, and A. G. Huntsman. When E. M. Walker invited him to the Go-Home Bay Biological Station on Georgian Bay in 1912, his career as a zoologist was determined. Here he carried out his first scientific investigations and, through careful rearing experiments, made substantial contributions to the life histories of many of the mayflies. These were published as a series of papers in the Canadian Entomologist (1913) thus commencing his scientific writing which still continues half a century later. These investigations of the mayflies of Georgian Bay led logically to Cornell University and research under James G. Needham.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

Following a Cornell doctorate in the spring of 1915 and a year of teaching zoology at the University of Maine, Dr Clemens joined the staff of the Department of Zoology at the University of Toronto where, for eight years — first as lecturer and then as assistant professor — he taught a variety of zoological subjects during the winter and did aquatic research during the summers. A. G. Huntsman introduced him to marine research and the marine fishes at the Atlantic Biological Station during the summer of 1918. Here, Dr Clemens and his wife investigated the muttonfish (*Zoarces anguillaris*) and this led to one of the first Bulletins of the Biological Board of Canada.

In 1920, B. A. Bensley established the Ontario Fisheries Research Laboratory of the University of Toronto. Dr Clemens was in charge of the field work and became the first director of its laboratory on Lake Nipigon. The many institutions entrusted to Dr Clemens have always been in better shape when he left than when he arrived and, during the next four years, fisheries studies in the University of Toronto and the Ontario Fisheries Research Laboratory gained a momentum which was in goodly measure responsible for its subsequent pre-eminent place among the biological institutions of Canada. It is a tribute to his capacity for leadership during this period that the nucleus of his staff in Nanaimo came from his Toronto classes and the summer workers at the Lake Nipigon field station. In the words of one of them "his approach in the field was to let us go and grow on our own, to let us work out our own salvation while quietly suggesting and advising so that one did not go too far astray and with it all there was a continuous interplay between the ideas of junior biologists and the mature scientists. His own work was carefully and systematically organized in the field, the lecture hall, and the laboratory and, in the latter, there was always the patient and deliberate effort to train students in thinking and discovering for themselves. Then, as now, there was the willingness to discuss and explore, to appreciate the attitude and needs of others, and to organize harmony within his own group and with others".

He brought the same philosophy to the Pacific coast when he came to Nanaimo in 1924 — rather uncertain of the wisdom of leaving pleasant and stimulating work in Ontario for the uncertainties of a remote fisheries station which was still largely a summer operation. He tells this story in his own way in the issue of this Journal marking the Fiftieth Anniversary of the founding of the Nanaimo Station.

The Nanaimo Station prospered under Dr Clemens and all of his initial appointees went on to positions of major responsibility in the fisheries work of this country. To this nucleus (R. E. Foerster, A. L. Pritchard, J. L. Hart), he soon added others and several of these came from the ranks of the summer volunteers. This group — some of them university students, others mature scientists from many different universities — found at Departure Bay a stimulating environment to which some were glad to return later on a permanent basis. By present-day research standards the Station had little to offer except space and the rich Pacific coast fauna; the demands for expensive field

work in distant places left little monetary support for the laboratory but Dr Clemens' unbounded and fresh enthusiasm for every aspect of natural history converted many to a lifetime of biological research. There was nothing amateurish in this enthusiasm, for Dr Clemens' philosophy has always been dominated by clear and courageous thinking and the centripetal importance of "a precise formulation of the problem". Much of the affection with which he is regarded by his former staff members in Nanaimo (and by many others in that community) is due to the unfailing courtesy and consideration that he showed to all and to his willingness to do sticky jobs himself while accepting responsibility for the shortcomings of others.

His contribution to fisheries science during this period was first of all that of a director; he selected his men with meticulous care, supported their projects as best he could and gave the quiet stimulation which enabled each of them to make a major contribution to the fishery of his particular concern. His personal research came second but has never been suspended at any time in his life; his numerous contributions to the life-history of the sockeye salmon, partly in collaboration with his wife Lucy, and his "Fishes of the Pacific Coast of Canada", in collaboration with G. V. Wilby, are fruitful results of this period. The latter — now in its second edition — was published after he left Nanaimo but the ground work was done there. It has found a place on more book shelves than any other publication of the Fisheries Research Board of Canada; to a host of the younger fisheries biologists, Dr Clemens' name is synonymous with a well-worn copy of this book.

During the first years of the Nanaimo directorship, Dr Clemens became closely involved in the establishment of the Board's Fisheries Experimental Station at Prince Rupert. He was nominally responsible for it during its first year until D. B. Finn became the Director in 1926 and continued to exert his influence as a member of the Fisheries Research Board of Canada (1943–1957). During the past five years he has again exercised his rare capacity for sparking productive co-operative ventures with the studies of the biochemical changes in the migrating salmon, undertaken jointly by the Board's Technological Research Laboratory in Vancouver (formerly the Fisheries Experimental Station) and the International Pacific Salmon Fisheries Commission.

Dr Clemens met his third great challenge as organizer and institution builder when, in 1940, he became Professor and Head of the Department of Zoology in the University of British Columbia. At the age of 52, this may have beckoned as a more restful environment with a return to the satisfying teaching experiences of earlier years. The decision, however, was taken at the beginning of a great war and an atomic age which soon pushed the universities of Canada into an unexpected period of expansion and growth. The years which followed were the most difficult in Canadian university history and, for Dr Clemens, the most demanding in time and effort. Particularly in the immediate post-war years, long lines of eager men waited their turn for that individual counsel and that scrap of paper on which they carried away a program of studies for the next few years.

His administration of the Department of Zoology was remarkably efficient although imperceptible. Beyond the universal respect which he has in full measure from his colleagues and former students, he will long be remembered at the University for the dynamic part which he played in the establishment of the Ph.D. program and for his imagination in fostering the Institute of Oceanography (established in 1949) and the Institute of Fisheries (established in 1953). He guided both of these through their infancy and is still an active participant in their seminars and a valued adviser on their problems.

The period of Dr Clemens' active headship in the Zoology Department was marked by two other major contributions in the fisheries field. The first of these stemmed from his co-operation with the British Columbia Game Commission (later the Fish and Game Branch, Department of Recreation and Conservation), eventually resulting in joint appointments between the Game Department and the University Department of Zoology. The association was most productive; it provided valuable research training for students and contributed vastly to the biology of British Columbia fish and game. The second was his chairmanship of the Saskatchewan Royal Commission on Fisheries in 1946, leading to a 131-page report on the fisheries problems of that province in 1947.

Dr Clemens continued active teaching in the Department of Zoology for seven years after his retirement in 1953. He assumed the directorships of the Institutes of Oceanography (1953–1958) and Fisheries (1953–1955) in the same year. The Vancouver Public Aquarium opened its doors to the public in the spring of 1956; Dr Clemens became president and spent a very active year organizing committees and making the wise decisions necessary to the success of this operation. A year later, with a pattern established, he retired from yet another venture well on the way to success. These years of "retirement" have also been marked by an active and productive association with the International Pacific Salmon Fisheries Commission — both in an advisory capacity and as scientific investigator.

His published papers and books will long be used by fisheries scientists of the Pacific coast; his influence has extended into the work of the Fisheries Research Board of Canada on both oceans and has more particularly permeated all the fisheries institutions of the west. His teaching has influenced the destinies of many and his personal and scientific philosophy still comes through clearly and sharply to his associates and friends.

This issue of the Journal honours Wilbert A. Clemens — scientist, teacher and man.

W. S. HOAR

A New Species of Parasitic Copepod, *Caligus clemensi* sp. nov. (Caligoida: Caligidae), from Pelagic Fishes in the Coastal Waters of British Columbia[1]

By R. R. Parker and L. Margolis

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Adult females and males of *Caligus clemensi* sp. nov. from the body surface of British Columbia fishes are described. The known hosts are *Oncorhynchus kisutch, O. gorbuscha, O. keta, Clupea pallasi, Gasterosteus aculeatus, Hexagrammos* sp. and *Theragra chalcogrammus*. This is the only species of *Caligus* known from the coastal waters of British Columbia. "*Caligus gurnardi* Krøyer" of Fraser, 1920, is synonymous with the new species.

INTRODUCTION

In the spring of 1962 a study was initiated in the Fitz Hugh Sound area of British Columbia of the biology of the pink salmon (*Oncorhynchus gorbuscha*) during the marine phase of its life. This study involved marking of large numbers of fingerlings of these fish by removal of the ventral fins. To our amazement significant numbers of the young pink salmon already had been fin-clipped by nature; not only were ventral fins missing but others as well. On closer examination we discovered that early chalimus stage larvae of a caligid were attached to the fins and their source of nourishment was the fin membranes. Various stages of fin damage, up to complete removal, could be attributed to the activities of this larval copepod.

Initially it was assumed that these larvae represented the well-known salmon caligid, *Lepeophtheirus salmonis*. Continued observations soon brought to light the presence of late chalimus larvae and adults which were not *L. salmonis*, but rather a member of the genus *Caligus*. Furthermore it became possible to piece together a complete series of chalimus larvae of this species. In addition, there was present on the same population of pink salmon a much smaller number of other chalimus larvae, generally attached to the body rather than the fins, which proved to belong to *L. salmonis*.

Further study revealed that the same species of *Caligus* also attacked other pelagic fishes living in the same habitat as the pink salmon.

Because of the possible role of these *Caligus* larvae in causing mortalities of young pink salmon, special attention was directed to studying this copepod. As a preliminary step to the investigation of the life history, development, and ecology of this parasite and its effect on survival of fingerling salmon, its identification was undertaken. This in itself proved not to be an easy task. More

[1]Received for publication February 25, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

than 200 species have been named to the genus *Caligus* (Yamaguti, 1963). Some of the named species are poorly described and, as indicated in a recent paper by Parker (1964), misidentifications, even by such well-known copepodologists as C. B. Wilson and H. Krøyer, have added confusion to this large and unwieldy genus. At the present time, a systematic revision of *Caligus* is sorely needed.

In spite of the aforementioned difficulties we have compared our material with existing descriptions of all species and with actual specimens of several European species obtained from Dr Torben Wolff of the Zoological Museum of the University of Copenhagen and from Dr J. P. Harding of the British Museum (Natural History), London. We have been unable to identify the British Columbia species with any previously named species and hence we are describing it as new, for which we propose the name *Caligus clemensi* sp. nov. in honour of Dr W. A. Clemens.

Parker (1964) reviewed the records of *Caligus* from British Columbia and has noted that the only species hitherto reported from this area has been *C. gurnardi* Krøyer, 1863. This species was listed by Fraser (1920) as having been found on the following fishes: *Salmo gairdneri*, *Oncorhynchus keta*, *Sebastodes* sp., and *Clupea pallasi*. A comparison of some of Fraser's material from *Clupea pallasi* (obtained from Dr J. R. Adams of the University of British Columbia) with Krøyer's type specimens showed that Fraser's specimens were not *C. gurnardi*. Specimens in the U.S. National Museum from *Gasterosteus aculeatus* from the Nanaimo area, which had been identified by C. B. Wilson as *C. gurnardi*, also proved not to belong to this species. Both lots of material, however, were identical with our proposed new species. Thus, at the present time *Caligus clemensi* is the only species of the genus known from British Columbia.

The California specimens from *Hydrolagus colliei* and *Oncorhynchus tshawytscha* reported by Wilson (1908) as *C. gurnardi* have been re-examined through the courtesy of Dr T. E. Bowman, U.S. National Museum. As noted by Parker (1964) these specimens are not *C. gurnardi* nor are they *C. clemensi*.

Specimens were cleared and studied as whole mounts in glycerine. Examination was made with a compound microscope, using a conventional system for transmitted light or phase contrast illumination, at magnifications up to 540 diameters. Appendages were examined *in situ*, except the mandible which was dissected out. Figures were drawn with the aid of a camera lucida.

DESCRIPTION OF *CALIGUS CLEMENSI* sp. nov.

FEMALE

COLOUR. The body is transparent but has a pink tint due to the large number of scattered red chromatophores. The egg sacs are conspicuously pinkish.

SIZE. The total length of the holotype female, including the caudal rami but excluding the anterior hyaline border and spination, is 4.35 mm. The midline length of the carapace is taken as standard length (l) and relative body proportions, given as decimal fractions of standard length, are presented in Table I. An outline drawing from the dorsal view is presented in Fig. 1.

TABLE I. Relative body proportions of the holotype female and allotype male of *Caligus clemensi* sp. nov., in terms of the midline length of the carapace having the value 1.00.

Body Part	Midline length		Maximum width	
	Holotype ♀	Allotype ♂	Holotype ♀	Allotype ♂
Total length	1.82	1.63		
Carapace	1.00	1.00	0.78	0.81
Cephalic area	0.54	0.50	0.78	0.81
Thoracic area	0.46	0.50	0.54	0.62
Free segment	0.06	0.08	0.25	0.20
Genital segment	0.46	0.27	0.44	0.24
Abdomen (total length)	0.31	0.28	0.14	0.18
First segment	0.28	0.07	0.14	0.18
Second segment		0.17		0.15
Caudal ramus	0.08	0.08	0.05	0.05
Fourth legs	0.40	0.37	0.04	0.03

The *frontal plates* together form a shallow convex arc bordered on the anterior margin by a narrow (0.015*l*) hyaline edge extending laterally and posteriorly to the first antennae and broken at the midline by a narrow sinus. A small spinule originates about $\frac{2}{3}$ the distance along the frontal plates from the midline to the lunules. The lunules are semi-circular and prominent, about 0.11*l* diameter.

The *cephalic* and *lateral* areas are bounded laterally and caudally by a wide (0.003*l*) hyaline border originating at the medial margins of the first antennae. A small spinule is present on each lateral edge approximately $\frac{2}{3}$ the distance from the origin of the hyaline border to its posterior terminus. Caudal and medial of these spinules a second pair is located on the dorsal surface, near to and projecting over a deep crescent-shaped depression on the dorsal surface. The lobes of the lateral areas are nearly of equal length to but three times the width of the thoracic lobes. The thoracic sinuses are narrow and open posteriorly. The *thoracic* area is nearly circular in outline and the posterior edges of the second and third sternae are ciliated.

The *free thoracic* segment is incompletely divided from the genital segment. The *genital* segment is rounded anteriorly with the lateral margins tapering posteriorly. The posterolateral corners are acute with concave posterior margins.

The *abdomen* is one-segmented with the posterolateral angles about 45° to the anal opening at the midline. A minute spinule is located on each lateral edge $\frac{1}{4}$ of the segment length caudally.

1st antenna (Fig. 2). The proximal segment bears 25 heavy plumose setae, arranged mainly in two parallel rows along the lateral margins[2]. The largest seta, originating at the apex, underlies and slightly exceeds the distal segment

[2]The terms medial and lateral margins refer to the endopodite and exopodite sides, respectively, of the appendages. *In situ* these are not always medial or lateral to the body axis.

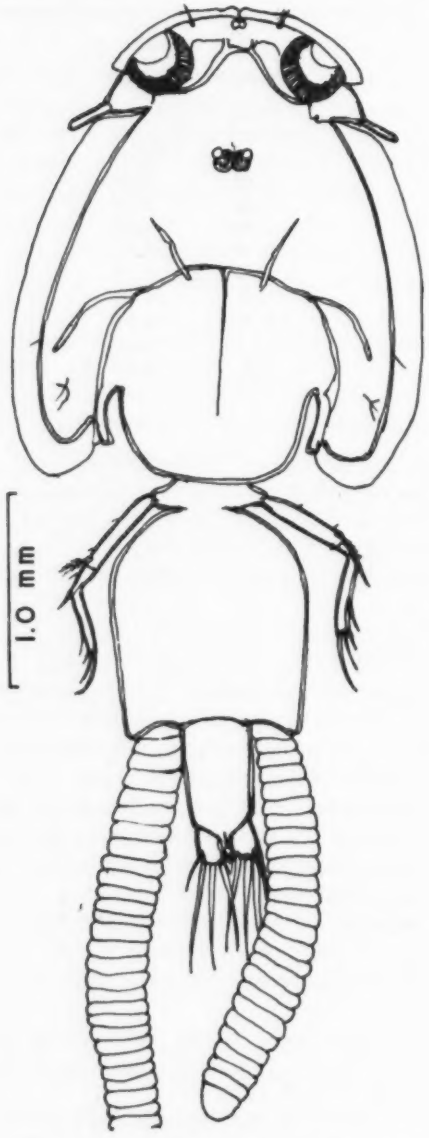


FIG. 1. *Caligus clemensi* sp. nov., holotype female. Dorsal view.

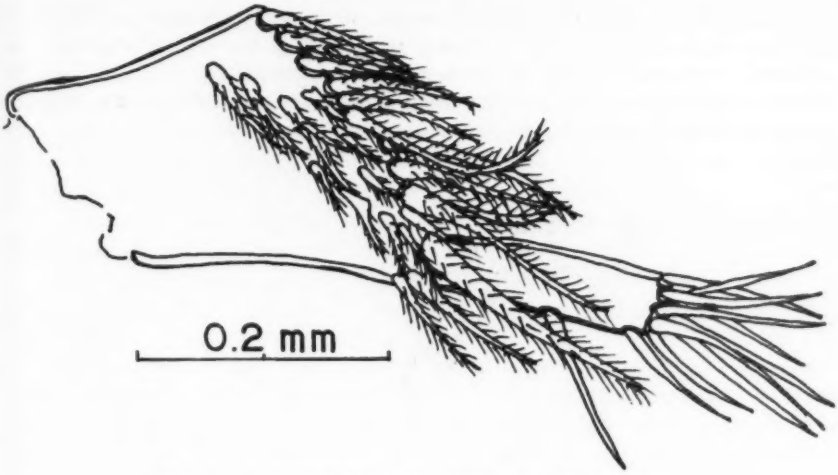


FIG. 2. *C. clemensi*, holotype. 1st antenna, ventral view.

in length. The distal segment is armed with 12 stiff, smooth apical setae and one similar seta originating $\frac{2}{3}$ the segment length distal on themedial margin.

The *2nd antenna* (Fig. 3a) is 4-segmented. The proximal segment bears a sharp triangular spine which points caudally toward the 2nd maxilla. The margin of the 2nd segment is produced into a triangular projection which also points caudally. A short spine originates near the base of the third segment and another near the apex on the lateral margin. The distal segment is modified into a stout claw which, *in situ*, hooks sharply toward the midline and bends ventrally away from the body surface.

The *mandible* is 4-segmented, the distal segment (Fig. 3j) being modified into a small hook directed, in the mouth tube, medially. The medial edge of the hook is serrated to form 11 or 12 slightly curved tooth-like processes.

The *1st maxilla* (Fig. 3b) is modified into a single smooth, curved spine. Near its base lies a papilla from which arise two to four hair-like setae. A short distance distally, a second papilla gives rise to three hair-like setae. Medial and slightly posterior of the base, on the sternum, a third papilla gives rise to a pair of heavier hair-like setae.

The *2nd maxilla* (Fig. 3c) is broad at the base and forms a smooth sharp hook directed ventrocaudally. Near its base a papilla gives rise to three closely applied spinules directed ventrally.

The *1st maxilliped* (Fig. 3d) appears to be 3-segmented. The proximal segment is shorter but stouter than the middle segment. A broad flat ciliated spine originates about $\frac{2}{3}$ of the segment length distally on the medial edge of the middle segment and terminates some distance proximal to the articulation of the middle and distal segments. The distal portion of the middle segment is prolonged beyond the point of articulation with the distal segment as a delicate

claw which is fringed with a ciliated membrane around its margins. The distal segment forms a chela with the distal projection of the middle segment. A ciliated membrane is present on the margins of approximately the distal $\frac{2}{3}$ length of the distal segment and forms a trough which is convoluted as the segment twists near the distal end (Fig. 3e).

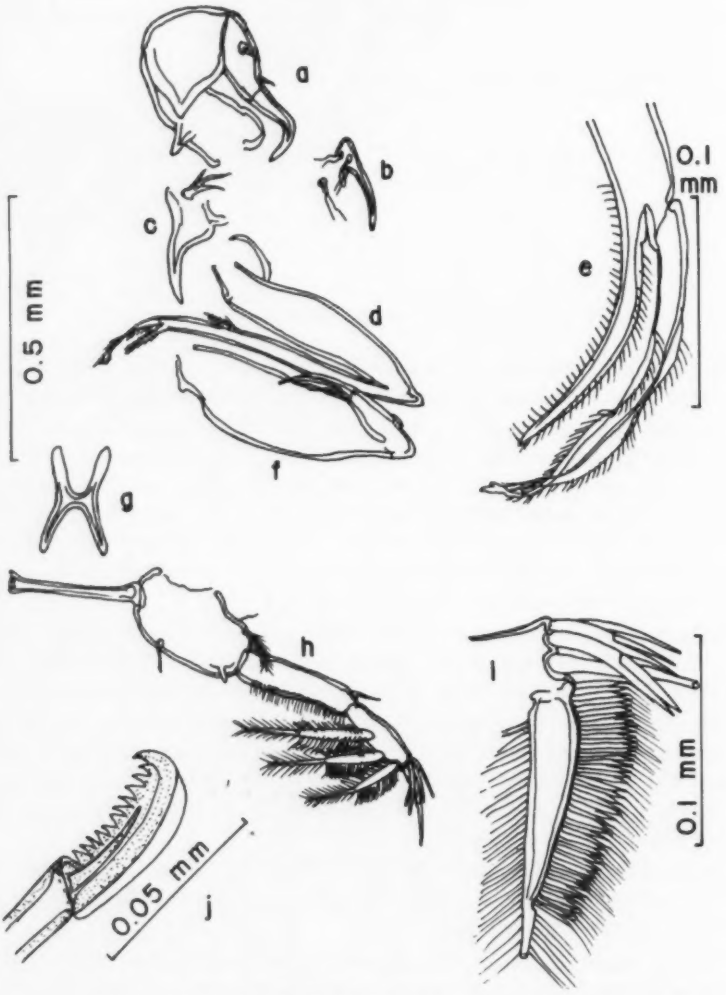


FIG. 3. *C. clemensi*, holotype. Cephalic and 1st thoracic appendages, ventral view *in situ*. a) 2nd antenna, b) 1st maxilla, c) 2nd maxilla, d) 1st maxilliped, e) enlarged view of tip of 1st maxilliped, f) 2nd maxilliped, g) sternal furca, h) 1st thoracic appendage, i) enlarged view of tip of 1st thoracic appendage, j) distal segment of mandible.

The *2nd maxilliped* (Fig. 3f) appears to be 3-segmented. The proximal segment is moderately stout and bears a single short spinule arising from a papilla on the medial surface $\frac{3}{4}$ the segment length distal from the base. The middle and distal segments are immovably fixed (although the suture is prominent) and together they form a stout claw which is slightly curved and articulates with the proximal segment. An apically directed spine originates near the base of the distal segment.

The *sternal furca* (Fig. 3g) is H-shaped, the rami are thin, slightly curved, little tapered, and slightly divergent from the base.

The *1st thoracic appendages* (Fig. 3h) are 3-segmented. The proximal segment is armed with a smooth spine about $\frac{1}{4}$ the segment length distal near the medial edge. A plumose seta originates at the laterodistal corner. The endopod is represented by a short round papilla on the mediodistal corner. The middle segment is ciliated along the medial edge and armed with a short smooth spine on the laterodistal corner. The distal segment is armed with four apical spines (Fig. 3i) of which the lateral one is simple. Both middle spines are supplied with accessory spines originating at about the midpoint which together with the primary spines form minute chelae. The medial (4th) spine is simple but about twice the length of the preceding three. The medial margin is armed with three large setae, the distal one about equal in length to the middle segment. These appear to be 2-segmented. Along the lateral margin of the proximal half, a row of large cilia with flattened bases gives the appearance of a picket fence. The medial edges and the lateral edges of the terminal sections are fringed with rows of simple but long cilia.

The *2nd thoracic appendages* (Fig. 4) are biramous. The *protopodite* is 2-segmented, the proximal segment small and bearing a large plumose seta on the mediodistal corner and a small smooth seta on the ventral surface. The distal segment is much expanded, bears a row of cilia along its medial margin, a small plumose seta and a ciliated membrane on the laterodistal corner and a simple seta on the ventral surface proximal and medial from the centre. The *exopodite* is 3-segmented, the proximal segment is the largest, bearing a large plumose seta on the mediodistal corner and a heavy smooth spine on the laterodistal corner. The middle segment is similarly armed; however, the plumose seta is much heavier and three times as long while the smooth spine is but $\frac{1}{2}$ as large as the corresponding members of the proximal segment. The distal segment is armed along the medial border with five plumose setae, similar to but shorter than the one on the middle segment. The cilia of these setae appear to be of two types; those on the proximal half are noticeably heavier than those on the distal portion. The distal end of the terminal segment is armed with a shorter seta which is ciliated along the medial border and possesses a serrated membrane along the lateral border. Lying close to this seta, on the distolateral margin, are two small, flattened and unequal spines, the distal being three times as large as the proximal. The *endopodite* is 3-segmented, the proximal segment bearing a long plumose seta at the distomedial corner and a patch of cilia on the distolateral corner. The middle segment bears two long plumose setae on the distomedial corner and

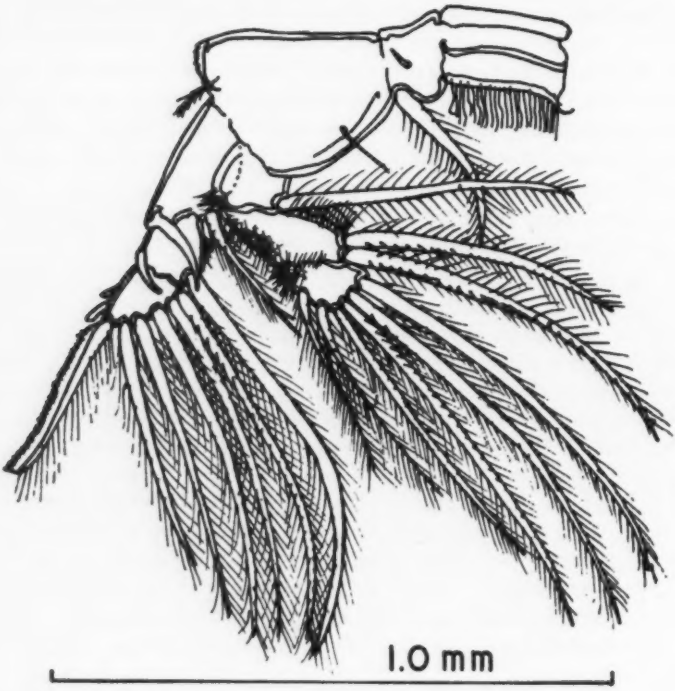


FIG. 4. *C. clemensi*, holotype. 2nd thoracic appendage, ventral view.

multiple rows of cilia on the lateral edge. The distal segment is armed with six plumose setae, four along the distal margin, one on the distolateral corner and one on the lateral margin. The proximolateral corner is densely ciliated.

The *3rd thoracic appendages* (Fig. 5) are biramous. The *protopodite* is indistinctly 2-segmented, greatly expanded and fused with the thoracic region. The lateral margin of the apical segment bears a wide ridged membrane, apparently of fused cilia with free terminal ends. Parallel to this membrane and on the ventral surface near the lateral edge, a secondary row of tiny cilia is present. This row returns proximally in a loop for a short distance. The distal end of the protopodite is ciliated along its broad margin between the rami, and the medial edge is ciliated and bears a simple seta in both the apical and proximal corners. The medial edge of the protopodite is ciliated and bears a large plumose seta on the proximal corner. The *exopodite* is 3-segmented. The proximal segment is very small, bearing a large thick smooth spine on the ventro-apical edge and a small spine on the midlateral edge. The middle segment is the largest and is densely ciliated along the lateral border. A small spine originates from the distolateral corner. The medial edge is smooth and armed with a large plumose seta on the distal corner. The distal segment is densely ciliated along the lateral margin and three simple small spines originate at the distolateral edge.

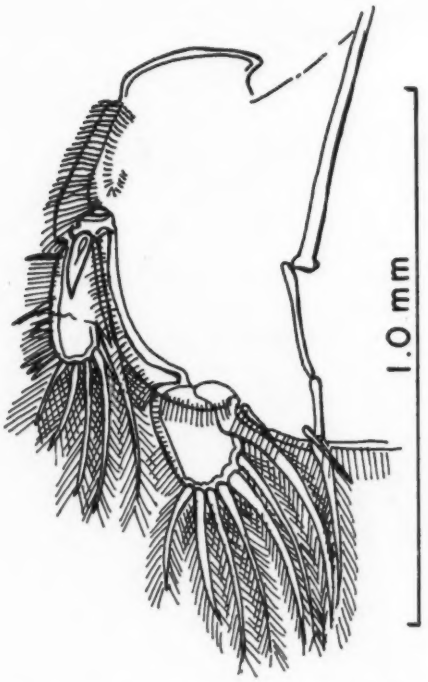


FIG. 5. *C. clemensi*, holotype. 3rd thoracic appendage, ventral view.

The distal edge is armed with four large plumose setae which increase in length medially. The *endopodite* is 2-segmented. The proximal segment is very short and armed medially with a large plumose seta. The distal segment bears six large plumose setae along the distal border which increase in size medially; the lateral margin is thickly ciliated and the medial margin is smooth.

The *4th thoracic appendages* (Fig. 1, 6a) are uniramous and 3-segmented. The proximal segment is the longest and bears a small plumose seta on the dorsal surface at the distolateral margin and two very minute spinules on the lateral margin which divide the segment roughly into three equal parts. The middle segment is short, bears a minute spinule at the midlateral margin and a stiff thick spine projecting apically from the distolateral corner. The base of this spine is surrounded by a poorly defined pectinated membrane. The distal segment articulates somewhat medially along the apical portion of the middle segment and is armed with four stiff spines, each bearing one or more rows of minute spinules. The first seta, of medium length, originates midway along the lateral margin. The second and shortest originates at the distolateral corner. The third, of medium length, originates at the midline on the distal edge and the fourth, which is much the longest, at the distomedial corner. Four pectinated

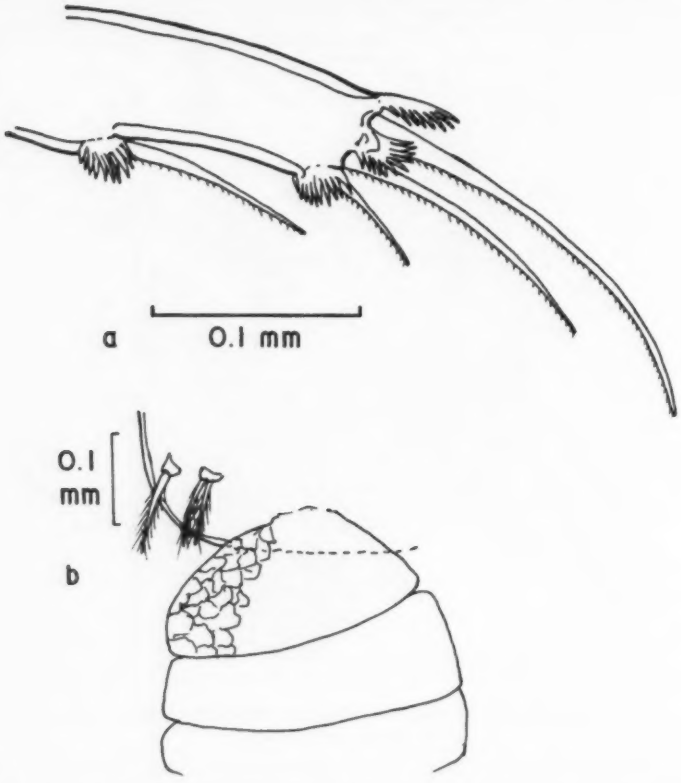


FIG. 6. *C. clemensi*, holotype. a) tip of 4th thoracic appendage, ventral view, b) 5th thoracic appendage, ventral view.

membranes are associated with these spines, the first and second covering the ventral bases of the first and second spines. The third covers the base of the fourth spine on the ventral surface and the fourth extends the medial and dorsal sides of the distolateral border. The fourth legs, excluding apical spines, are slightly shorter than the genital segment.

The *5th thoracic appendages* (Fig. 6b) are not prominent from the dorsal view. They are represented by a single plumose seta arising from a short papilla on each ventrolateral surface of the genital segment a short distance from the distolateral corner and two smaller plumose setae arising from a second papilla located medioventrally from the first.

The *caudal rami* (Fig. 7) are about as wide as long, the medial borders being somewhat shorter than the lateral borders due to the angle of articulation with the abdomen. They are each armed with three small and three large plumose setae. Of the former, the first and smallest originates on the midventral surface

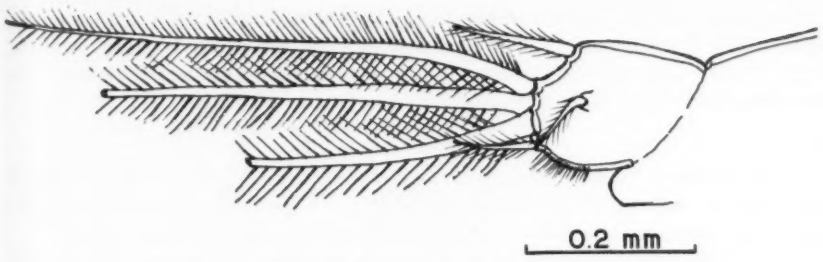


FIG. 7. *C. clemensi*, holotype. Caudal rami, ventral view.

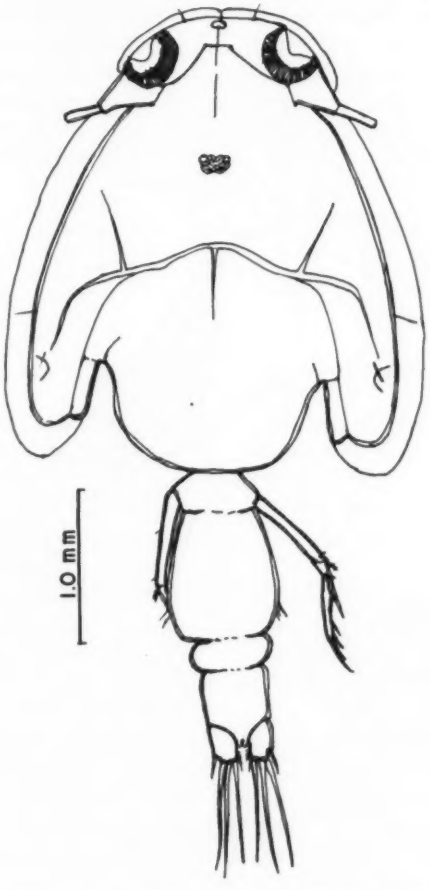


FIG. 8. *C. clemensi* sp. nov., allotype male. Dorsal view.

and typically points medially, while the remaining two occupy the posteromedial and posterolateral corners. The large setae originate on the posterior or distal edge. The middle seta is the longest, the remaining two are nearly equal. The posteromedial edges of the caudal rami are covered with dense cilia.

MALE

The allotype male is illustrated in dorsal view in Fig. 8 and relative measurements of body parts are given in Table I. Total length including caudal rami but excluding the anterior hyaline border and spination is 4.83 mm.

In addition to differences in relative body proportions, the male differs from the female by possessing a 2-segmented abdomen.

The *1st antennae* are similar in every respect to those of the female.

The *2nd antennae* (Fig. 9) are highly modified. The triangular spine is absent from the basal segment. The middle segment has a transverse groove on the ventral surface and the area surrounding this groove and distal to it is covered with a series of file-like ridges which also continue proximally along the dorsal surface of the medial edge. The third segment (Fig. 10) is modified into a broad and wrinkled flap which turns back on the second segment for a short distance.

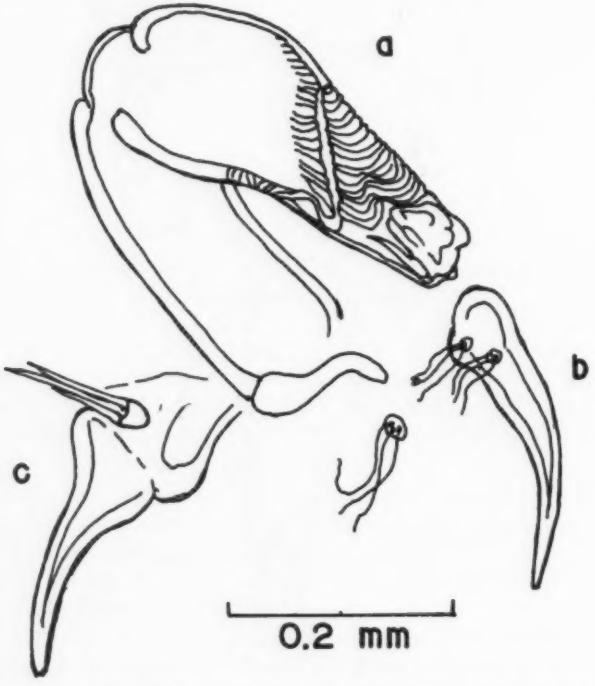


FIG. 9. *C. clemensi*, allotype. a) 2nd antenna, b) 1st maxilla, c) 2nd maxilla. Ventral view *in situ*.

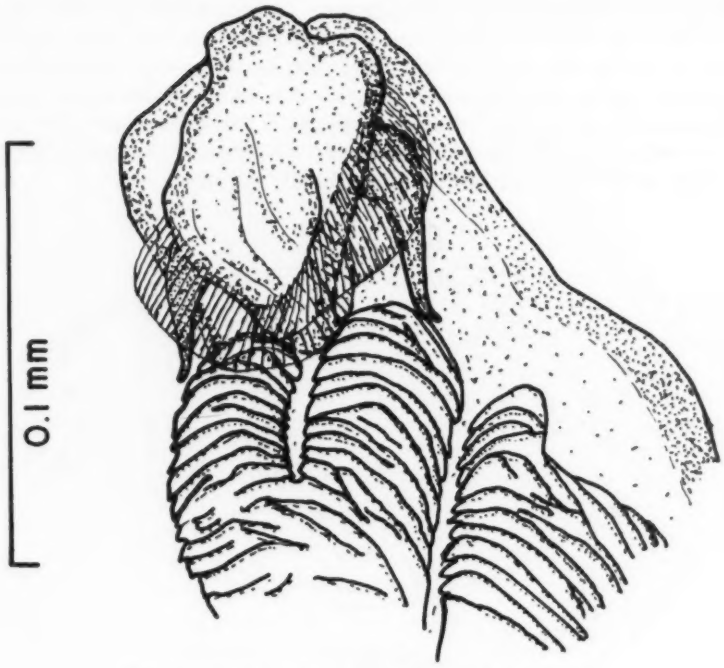


FIG. 10. *C. clemensi*, allotype. Tip of left 2nd antenna.

A small curved spine originates on each of the lateral and medial edges of the third segment and is directed proximally. Associated with this segment are two membranes; one originates at the midlateral edge and extends around the tip of the segment to the medial edge and the other originates proximally on the medial edge and also extends around the tip of the segment, partially overlying the lateral membrane.

The *mandibles* are similar to those of the female. The *1st maxillae* (Fig. 9) are similar to those of the female but relatively about twice as large. The *2nd maxillae* and *1st maxillipeds* (Fig. 9) also are similar to those of the female. (The tip of the right 2nd maxilla of the allotype male is slightly bifurcate. This is, however, not a constant character.)

The *2nd maxillipeds* (Fig. 11) are modified to form powerful grasping organs. The basal segment is wider and thicker than that of the female, and, on the posterior side, the distomedial corner is produced into a short triangular spine with a crenulated ridge leading apically from it. On the medial margin, proximal to this crenulated ridge, a short spinule originates from a circular papilla. On the distal edge, lateral to the crenulated ridge, a second triangular spine-like process is found. On the anterior surface a round patch of tubercles lies close to the distomedial corner. The middle and apical segments, like those of the

female, are formed into a stout claw, bearing on its posterior surface, just proximal of the suture line between these two segments, a short spine originating from a circular papilla. On the apical segment, near the proximomedial margin, a relatively long spine originates which roughly parallels the apical segment. On the anterior surface of the middle segment a triangular depression extends from the midmedial towards the lateral edge. A small round papilla is located proximally on the posterior surface of the middle segment.

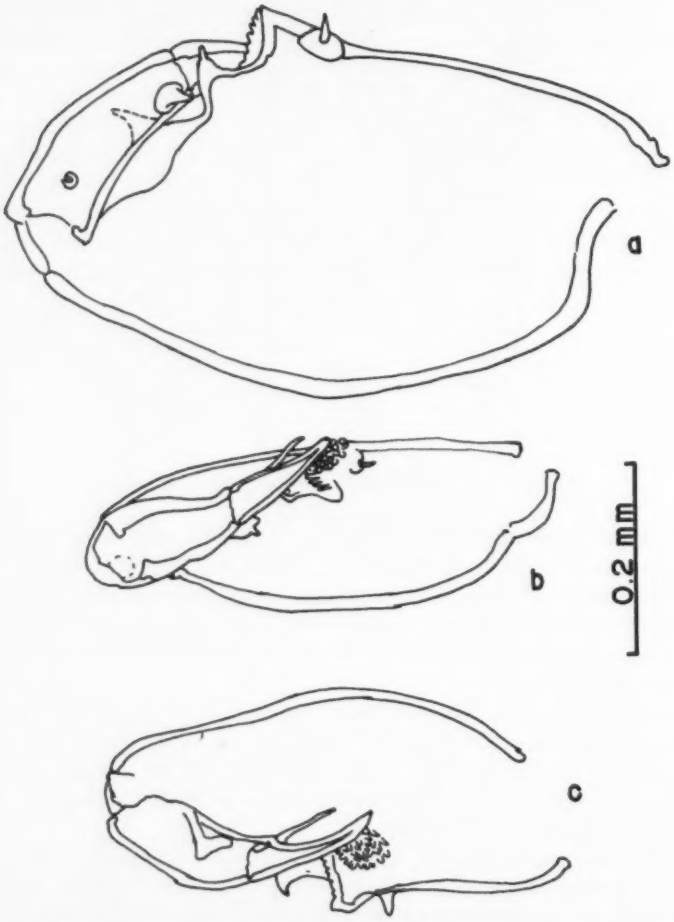


FIG. 11. *C. clemensi*. 2nd maxilliped in male. (a) *Allotype*. Appendage tipped forward, posterior side shown, medial edge of protopodite at top; (b) *Paratype male* (3.6 mm body length). Appendage in normal position, medial edge of protopodite shown; (c) *Paratype male* (3.9 mm body length). Appendage tipped caudally, anterior side shown, medial edge of protopodite at bottom.

The first *five pairs* of *thoracic appendages* are similar to those of the female. The male possesses, on the ventral surface of the genital segment, two sets of three minute spines (Fig. 12), taken as vestiges of a sixth pair of thoracic appendages. A minor difference is noted between the location of the ventral ciliated setae on the caudal rami; for the males these setae originate slightly lateral from the equivalent position on the female, and point caudally.

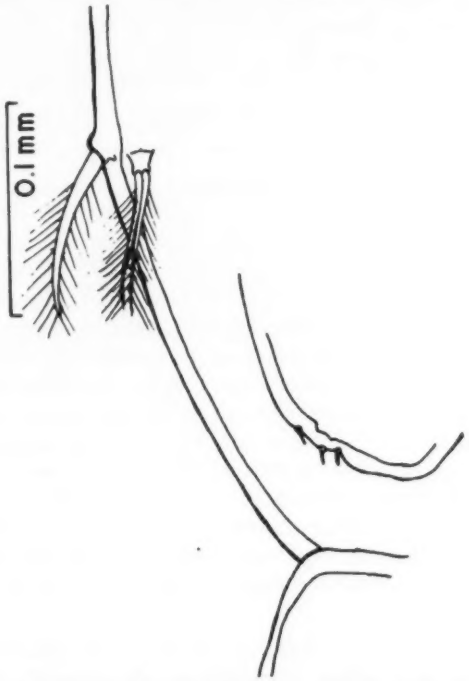


FIG. 12. *C. clemensi*, allotype. 5th and 6th thoracic appendages, ventral view.

Hosts: juvenile *Oncorhynchus gorbuscha* (Walbaum), pink salmon;
juvenile *O. kisutch* (Walbaum), coho salmon;
juvenile *O. keta* (Walbaum), chum salmon;
juvenile and adult *Clupea pallasi* Valenciennes, Pacific herring;
juvenile *Hexagrammos* sp., greenling;
juvenile and adult *Gasterosteus aculeatus* Linnaeus, threespine sticklebeck;
adult *Theragra chalcogrammus* (Pallas), whiting (only found on one host).

Location on host: External body surfaces; chalimus larvae attached to fins, rarely to body.

Type locality: Fitz Hugh Sound area, central British Columbia coast.

Other locality: Vicinity of Nanaimo, Vancouver Island, British Columbia.

Type specimens: Holotype female from a juvenile *O. kisutch* collected June 13, 1962, in Fitz Hugh Sound; allotype male from a juvenile *O. gorbuscha* collected June 8, 1962, in Fitz Hugh Sound.

Holotype (Cat. No. 6954), allotype (Cat. No. 6955), six female and six male paratypes (Cat. No. 6956) deposited in the National Museum of Canada, Ottawa, Canada. Three female and three male paratypes also deposited in each of the Zoological Museum of the University of Copenhagen, the British Museum (Natural History), London (B.M. Reg. 1964.2.27.1), the U.S. National Museum, Washington, D.C. (USNM Cat. No. 111010), and the Department of Zoology, University of British Columbia. Other paratypes are in the authors' collection at the Nanaimo Biological Station.

DISCUSSION

There are many similarities between *C. clemensi* and *Caligus rapax* Milne-Edwards, 1840 of Baird, 1850 and later authors. (It is debatable whether the *C. rapax* described by Milne-Edwards is identical with the species described under this name by later workers.) Among the distinguishing characteristics the following can be readily observed: (1) the lunules of *C. clemensi* are about twice the diameter of those in *C. rapax* of similar body length; (2) differences in the relative lengths of the spines on the distal segment of the 4th thoracic appendage; (3) the small, subterminal seta on the caudal rami originates midventrally in *C. clemensi*, whereas it originates near the distolateral corner in *C. rapax*; (4) the 6th leg in the male of *C. rapax* is represented by a pair of plumose setae, whereas in *C. clemensi* it is reduced to 3 simple minute spines; and (5) the distomedial margin of the male 2nd maxilliped is, in *C. rapax*, simple and unadorned, whereas in *C. clemensi* this margin is armed with spines, a patch of tubercles, and is otherwise sculptured.

The known hosts of the chalimus larvae and adults of *Caligus clemensi* belong to three orders of fishes: Clupeiformes (*Oncorhynchus* and *Clupea*), Perciformes (*Hexagrammos*) and Gasterosteiformes (*Gasterosteus*). Adults have been taken from a representative of a fourth order, namely Gadiformes (*Theragra*). In addition, *Salmo gairdneri* and *Sebastodes* sp. (Perciformes), from which Fraser (1920) reported "*C. gurnardi*", should probably also be regarded as hosts of *C. clemensi*. This range of hosts would indicate a lack of phylogenetic host specificity. On the other hand all the hosts were captured in the surface layer of sheltered coastal waters. The parasite has not been found on benthic or open water pelagic fishes. Even the infected *Theragra* was captured at the surface near shore; this fish was found floating at the surface in an obviously diseased condition. It appears, then, that *C. clemensi* is specific for a given type of environment and may attach to any species of fish living in that environment.

It is interesting that only one species of *Caligus* is known from the marine waters of British Columbia, although the genus consists of more than 200 species. In contrast, the closely related *Lepeophtheirus* is represented in British Columbia

by at least eight species (Wilson, 1912; Fraser, 1920) and has been found on pelagic and benthic fishes. In terms of the number of species, *Caligus* has been singularly unsuccessful on the Pacific coast of Canada. However, in terms of numbers of individuals of *C. clemensi*, it has prospered in a particular segment of the environment, being especially abundant on juvenile salmon, herring and stickleback.

REFERENCES

FRASER, C. M. 1920. Copepods parasitic on fish from the Vancouver Island Region. *Trans. Royal Soc. Canada*, Ser. III, **13**: 45–67.

PARKER, R. R. 1964. A review and redescription of *Caligus gurnardi* Krøyer, 1863 (Copepoda: Caligidae). *Crustaceana* (submitted for publication February 1964).

WILSON, C. B. 1908. North American parasitic copepods: a list of those found upon the fishes of the Pacific coast, with descriptions of new genera and species. *Proc. U.S. National Museum*, **35**: 431–481.

1912. Parasitic copepods from Nanaimo, British Columbia, including eight species new to science. *Contr. Can. Biol.*, 1906–1910: 85–101.

YAMAGUTI, S. 1963. Parasitic Copepoda and Branchiura of fishes. Interscience Publishers. New York, London and Sydney.

Preliminary Observations on the Vertical Distribution of Pacific Salmon (Genus *Oncorhynchus*) in the Gulf of Alaska[1]

By J. I. Manzer

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

The vertical distribution of Pacific salmon in the high-seas areas of the Gulf of Alaska was investigated from mid May through July in 1959 and 1960 by fishing with gillnets (constructed from 4½-inch nylon web and measuring 40 ft in depth and initially 400 fathoms in length) at five depth intervals from the surface with the deepest between 160 and 200 ft.

Sockeye salmon exhibited diurnal and seasonal differences in their vertical distribution while chum salmon showed diurnal differences. The downward movement of sockeye salmon appeared limited by the thermocline, especially during late June and July. This relationship was observed for chum salmon during hours of darkness only in late June and July. Other factors must also influence seasonal and diurnal vertical movements of sockeye and chum salmon. Within the conditions of the experiment, no consistent differences in the vertical migrations between fish of different age were apparent. Catches showed pink and coho salmon were nearer the surface than either sockeye or chum salmon.

INTRODUCTION

Prior to 1954, relatively little was known of the distribution of salmon (genus *Oncorhynchus*) in the Subarctic North Pacific Ocean. Since then information has been accumulating rapidly, principally as a result of studies undertaken by Canada, Japan, and the United States as member nations of the International North Pacific Fisheries Commission. To a large extent, research studies have been concerned with horizontal distribution of salmon taken in the immediate surface layers during the spring and summer months. Little effort, by comparison, has been directed toward studying vertical distribution and related factors, although it has been generally recognized that such information was pertinent to interpretation of surface catches.

This paper describes the results of preliminary studies on vertical distribution of salmon conducted by the Nanaimo Station of the Fisheries Research Board of Canada in 1959 and 1960 in the Gulf of Alaska region.

METHODS AND GEAR

The principal objective of field work in 1959 was to determine temporal and regional differences in vertical distribution of salmon. To this end, fishing was conducted in three areas of the Gulf of Alaska, namely the northwest (Station 2), central (Stations 1 and 4), and southeast (Station 3) areas (Fig. 1). These areas were selected on the basis of data on distribution of salmon in surface waters

[1]Received for publication June 3, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

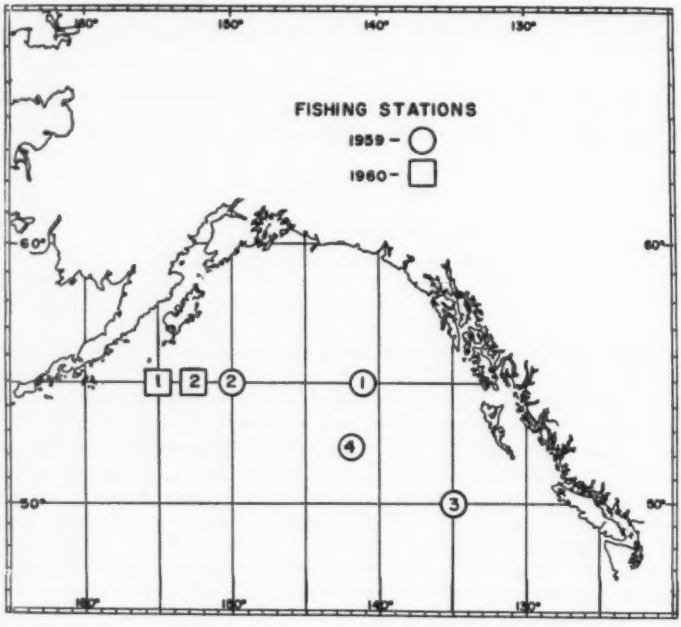


FIG. 1. Fishing stations in the Gulf of Alaska, 1959 and 1960.

for previous years, which showed that sockeye and chum salmon throughout the season were relatively more numerous in the northwest part of the Gulf. Fish were present in the southeast area in May, but were absent at least from surface waters after mid July when seasonal warming occurred (International North Pacific Fisheries Commission, 1958 and 1959; Manzer *et al.*, 1964). It was not known whether this absence of salmon was due to horizontal evacuation from waters having relatively high temperatures or to vertical withdrawal into strata having relatively colder temperatures.

Observations in 1959 were first made on May 13 and, except for interruptions resulting from gear damagé or port calls, were continued to August 1. Fishing was conducted at a series of depths in one area before moving to another. The time spent on any one fishing series never exceeded 7 days. Fishing was mainly conducted between the hours of dusk and dawn. In May, some fishing during daylight hours was attempted to obtain information on diurnal vertical migrations.

In 1960, the work was confined to the northwest area of the Gulf. Emphasis was mainly on diurnal and seasonal changes in vertical distribution, as observed at a single locality. Fishing was first carried out at Lat. 55°N, Long. 155°W. Relatively strong currents created operational difficulty and at an early stage in the program the study site was moved eastward to Lat. 55°N, Long. 152°W (Fig. 1) where fishing ceased on July 13. Fishing was conducted regularly during

the day as well as the night, otherwise the routine was reasonably similar to that of 1959.

The gear used in each year was essentially the same in design and construction. The main part was a nylon gillnet 40 ft (12.2 m) in depth made of 4½-inch (11.4-cm) mesh web (stretched measure). The net could be suspended from surface buoys by various sets of drop lines enabling fishing at five depth intervals of 40 ft with the deepest between 160 ft (about 49 m) and 200 ft (about 61 m). In conjunction with the "depth net", a surface gillnet 20 ft deep (6.1 m) and of similar mesh size was used. The latter net provided information on salmon in surface waters when the depth net was fished at depth. The depth net in each year was initially 400 fathoms (about 730 m) long. The surface net was initially 150 fathoms (about 275 m) long in 1959 and 300 fathoms (about 550 m) in 1960. Due to damage during fishing, the lengths of the nets were altered during the season (Tables I and II).

The standard fishing procedure was to set the two types of nets in tandem (the depth net farthest from the vessel) at the surface on the first night. On each consecutive night the depth net was lowered one depth interval (40 ft) until the greatest depth (160–200 ft) was reached. When observations were being made on diurnal movements of salmon a similar series was conducted during the day. On the average, day sets were for approximately 7 hr; night sets, approximately 9 hr.

Bad weather or other circumstances affected the number of fishing operations in some areas. The catches in some areas, particularly in 1959, were rather small. To overcome gaps in depth or day–night observations the catches in the northwest (Station 2) and central areas (Stations 1 and 4) of the Gulf in that year were combined to provide larger sample sizes. This procedure seemed justifiable since the two areas are somewhat similar in oceanographic properties (Doe, 1955; Dodimead *et al.*, 1963), and thus could influence vertical distribution of salmon in the same way.

Age determination (from scales) were made for sockeye and chum salmon caught in 1960 only. Catches of each species in 1959 for the most part were small and since several age-types were present age composition data were not considered.

Vertical temperature structure at each fishing site was obtained from bathythermograph casts to 270 m.

RESULTS

The catches and associated data for 32 sets in 1959 are shown in Table I, and for 29 sets in 1960 in Table II.

The catches by the surface net indicate in a general way the availability of salmon in waters within 20 ft of the surface. In most instances the surface net caught more salmon than the depth net, although differences in length, depth, and possibly tension of the two nets suggest that the catches are not strictly comparable. The catches by the depth net, set at various depths including the surface (0–40 ft), provide more reliable comparisons for inferring vertical distribution of the salmon.

TABLE I. Salmon catches made by the surface and depth nets at various fishing stations in the Gulf of Alaska, 1959. Station positions are shown in Fig. 1.

	Stn.	No. hours fished	Surface net						Depth net						
			Length (*fm*)	Species					Fishing depth (*ft*)	Length (*fm*)	Species				
				Sock-eye	Chum	Pink	Coho	Total			Sock-eye	Chum	Pink	Coho	Total
Day sets															
May 17	1	7.0	150	1	..	..	..	1	0–40	400	1	..	..	..	1
" 18	1	7.0	150	2	..	..	..	2	40–80	400	..	..	..	..	..
" 19	1	6.0	100	2	..	..	..	2	80–120	400	2	..	..	..	2
" 20	1	6.0	150	4	..	..	..	4	120–160	400	1	1	..	..	2
" 25	2	7.5			not set				0–40	400	..	..	..	..	..
" 26	2	8.0	150	1	1	..	..	2	40–80	400	1	6	..	..	7
" 28	2	6.0	100	..	..	..	..	..	120–160	400	5	1	..	..	6
Total				10	1	..	..	11			10	8	..	..	18
Night sets															
May 17	1	8.5	150	4	1	..	..	5	0–40	400	6	..	..	..	6
" 18	1	8.0	150	12	..	..	..	12	40–80	400	2	..	..	..	2
" 19	1	9.0	100	13	..	1	..	14	80–120	400	..	5	..	..	5
" 20	1	10.0	150	..	..	..	..	..	120–160	400	..	3	..	..	3
" 21	1	8.0	150	19	18	..	..	37	160–200	400	1	2	..	..	3
" 25	2	8.5			not set				0–40	400	4	1	2	..	7
" 26	2	8.5	150	4	..	..	..	4	40–80	400	1	2	2	..	5
" 27	2	13.5	150	3	2	..	..	5	80–120	400	3	..	..	..	3
" 28	2	8.0	100	7	..	..	..	7	120–160	400	..	..	..	..	..
June 10	2	9.0	100	9	3	..	..	12	0–40	400	16	1	2	1	20
" 11	2	9.0	100	5	..	3	1	9	40–80	400	3	1	6	..	10
" 12	2	7.0	100	5	..	..	..	5	80–120	400	..	..	1	..	1
July 5	3	8.0	50	..	..	..	..	..	0–40	350	6	..	1	..	7
" 6	3	8.5	50	2	..	..	..	2	40–80	350	..	..	..	1	1
" 7	3	8.5	50	1	..	..	..	1	80–120	350	..	..	..	..	..
" 10	3	9.0	150	4	..	..	1	5	120–160	350	..	..	..	..	..
" 11	3	9.5	150	11	..	..	..	11	160–200	350	..	..	..	..	..
" 15	4	8.0	150	1	3	6	..	10	0–40	350	3	6	11	..	20
" 18	4	8.0	150	1	..	2	..	3	40–80	350	..	2	..	..	2
" 19	4	8.5	150	5	2	2	..	9	80–120	350	..	..	..	..	..
" 20	4	8.5	150	1	6	1	..	8	120–160	350	..	..	..	..	..
" 21	4	8.5	150	..	2	2	..	4	160–200	350	..	..	..	..	..
" 25	2	8.0	150	3	1	3	..	7	0–40	350	13	24	14	1	52
" 26	2	8.0	150	6	25	2	..	33	80–120	350	..	..	..	..	..
Aug. 1	2	8.0	150	2	1	1	..	4	40–80	350	..	6	..	..	6
Total				118	64	23	2	207			58	53	39	3	153

TABLE II. Salmon catches made by the surface and depth nets during the day and night in the northwest area of the Gulf of Alaska, 1960.

	Stn.	No. hours fished	Surface net						Depth net						
			Length (*fm*)	Species					Fishing depth (*ft*)	Length (*fm*)	Species				
				Sock-eye	Chum	Pink	Coho	Total			Sock-eye	Chum	Pink	Coho	Total
Day sets															
May 17	1	6.5	300	19	6	..	..	25	0–40	400	10	4	..	..	14
" 18	1	5.0	300	4	2	..	..	6	40–80	400	3	6	..	..	9
" 19	1	6.0	300	6	1	..	..	7				net lost			
June 2	2	6.0	300	94	1	..	..	95	80–120	200	76	5	..	..	81
" 4	2	9.0	300	19	2	..	..	21	120–160	200	24	2	..	..	26
" 5	2	6.0	250	10	1	..	..	11	160–200	200	9	11	..	..	20
" 6	2	7.5			not set				0–40	200	5	3	..	..	8
" 7	2	6.0	250	4	1	..	..	5	40–80	200	12	4	..	..	16
" 22	2	8.0	250	3	..	..	..	3	160–200	200	..	1	..	..	1
" 23	2	6.0			not set				0–40	200	4	1	..	..	5
" 24	2	8.5	250	8	6	..	..	14	40–80	200	25	1	..	..	26
July 1	2	6.5	250	8	7	..	..	15	80–120	200	1	..	2	..	3
" 2	2	6.5	250	8	3	..	..	11	120–160	200	..	..	..	..	..
" 4	2	7.0	250	2	9	..	..	11	160–200	200	..	..	..	..	..
Total				185	39	..	..	224			169	38	2	..	209
Night sets															
May 18	1	11.0	300	14	5	..	..	19	0–40	400	15	2	1	..	18
" 19	1	9.0	300	13	3	..	..	16	40–80	400	2	26	..	..	28
June 3	2	8.5	300	54	1	..	..	55	80–120	200	38	3	..	..	41
" 4	2	9.0	300	52	4	..	..	56	120–160	200	1	..	..	..	1
" 5	2	9.0	250	29	5	..	..	34	160–200	200	..	..	..	..	..
" 6	2	11.0			not set				0–40	200	5	11	..	..	16
" 7	2	9.5	250	19	11	..	..	30	40–80	200	4	13	..	..	17
" 8	2	8.5	250	19	12	..	1	32	80–120	200	4	6	..	..	10
" 10	2	10.0	250	10	3	..	..	13	120–160	200	5	..	..	..	5
" 23	2	9.0	250	4	10	4	..	18	160–200	200	..	..	..	..	..
" 24	2	9.0			not set				0–40	200	11	2	..	..	13
July 1	2	9.5	250	21	3	..	..	24	40–80	200	15	12	15	..	42
" 2	2	11.0	250	29	18	43	1	91	80–120	200	..	10	7	..	17
" 4	2	9.0	250	17	4	16	..	37	120–160	200	..	..	..	..	..
" 5	2	7.5	250	23	5	1	..	29	160–200	200	..	..	..	..	..
Total				304	84	64	2	454			100	85	23	..	208

SOCKEYE SALMON (*O. nerka*)

Sockeye was the most numerous species in the catches, regardless of gear or part of the day fished. Figure 2 shows for various series of sets the percentage of sockeye salmon caught by the depth net at various levels during night and day according to area and time period in 1959 and 1960. The percentages are based on the average catch made by 400 fathoms of gillnet in the sets at each depth interval expressed as a percentage of the sum of the average catches made over the full depth range fished.

In the northwest Gulf of Alaska in the early period (Stations 1 and 2 combined, late May–early June), sockeye were present throughout the vertical range investigated, being taken during the night in 1959 and during the day in 1960 as deep as the 160- to 200-ft level. (They may well have been deeper.) In both years sockeye tended to be relatively more numerous at deeper levels during the day and at shallower levels during the night. This difference in relative numbers with depth and time of day is interpreted as diurnal vertical movements rather than avoidance of the net, through sight, in surface waters during the day. If sockeye did not undertake vertical movements but instead were at all times uniformly distributed through a column of water, the relative size of catches during the day and night at the deepest levels where visibility conditions are poor could be expected to be reasonably similar, which was not the case. In 1960, a considerable portion of the catch both by day and night was made at the 80- to 120-ft level, but the relatively large day-catch would seem exaggerated because the surface net fished at the same time indicated that sockeye were abundant at the 0- to 20-ft level (Table II).

Later in the season, in 1960, the diurnal vertical pattern of the early period was still evident but sockeye were shallower. Only one individual was caught below 80 ft, in a day set at the 80- to 120-ft level. This seasonal difference in vertical distribution was also suggested by night catches in the northwest Gulf area in 1959, although catches were smaller.

In the southeast area while all depths were fished during July 5–11, sockeye salmon were caught only in the 0- to 40-ft level.

The age composition of sockeye caught in the various fishing series in 1960 is given in Table III.

In each time period and type of gear, 4_2's[2] were the dominant age group. Combining surface and depth net catches for each period and time of day, as the season advanced 4_2's increased in importance (as did 5_3's, but not to the same extent) while 5_2's and 6_3's declined, largely reflecting the evacuation of maturing fish from the experimental fishing areas.

There is no evidence for consistent differences in vertical distribution, either diurnally or seasonally, among catchable sockeye of different total age or ocean age.

[2]A 4_2 sockeye represents a fish which has spent one complete growing season in fresh water, has migrated to sea in its second growing season (subscript 2), and was caught at sea in its fourth growing season after spending two winters in the ocean.

TABLE III. Age composition of sockeye salmon caught by the surface and depth nets during the day and night in the northwest area of the Gulf of Alaska, 1960.

Period		Surface net						Depth net					
	Age:	4_2	5_2	5_3	6_3	Other	Total	4_2	5_2	5_3	6_3	Other	Total
Day sets													
May 17–June 7													
No.		89	31	7	19	10	156	66	24	23	15	11	139
Percentage		57.0	19.8	4.8	12.1	6.3	100.0	47.5	17.3	16.5	10.8	7.9	100.0
June 22–July 4													
No.		14	7	3	3	2	29	20	4	4	..	2	30
Percentage		48.4	24.1	10.3	10.3	6.9	100.0	66.7	13.3	13.3	..	6.7	100.0
Night sets													
May 18–June 10													
No.		135	32	13	15	15	210	49	15	4	6	..	74
Percentage		64.4	15.2	6.2	7.1	7.1	100.0	66.2	20.3	5.4	8.1	..	100.0
June 23–July 5													
No.		68	9	8	2	7	94	16	3	5	..	2	26
Percentage		72.3	9.6	8.5	2.2	7.4	100.0	61.6	11.5	19.2	..	7.7	100.0

Bathythermograph casts showed minor variations in temperature profiles during the same fishing series. In the depth levels fished, considering all areas, temperatures ranged from 3.5°C to 12.3°C in 1959. Water temperatures were relatively lower in the northwest area of the Gulf than in the southeast. In 1960, during May 17 to June 10, temperatures in the northwest were slightly higher than in 1959 for roughly corresponding periods. In both years water temperatures increased through the study and a thermocline developed, a typical pattern for the eastern subarctic Pacific Ocean (Tully and Giovando, 1963). Profiles considered representative of vertical temperature conditions at each area and time period are shown in Fig. 2.

In the northwest area during the early fishing series in each year, temperature traces showed nearly isothermal conditions from the surface to about 40 m, a slight thermocline between 40 m and about 160 m, and nearly similar temperatures

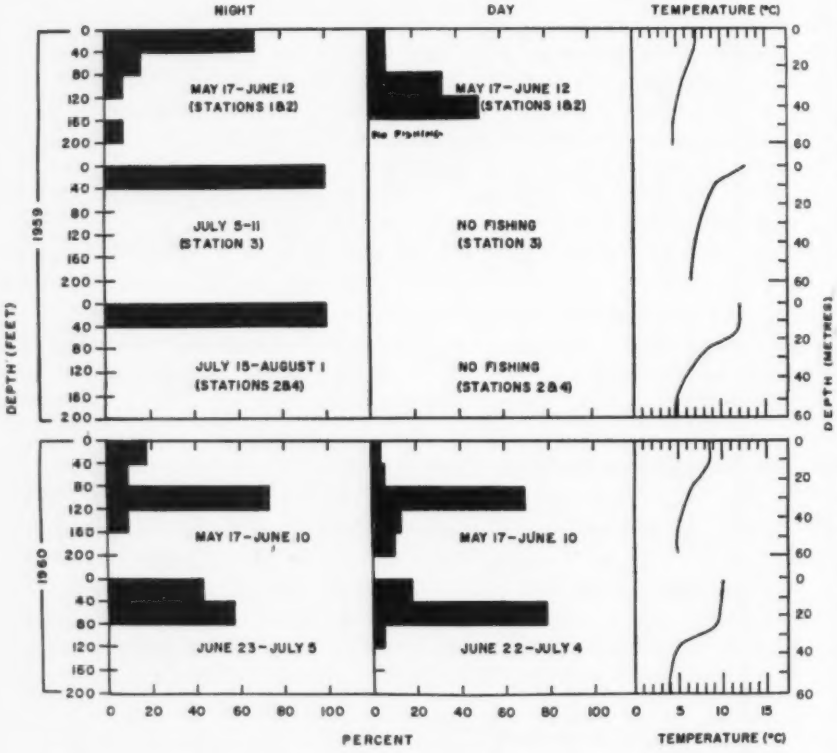


FIG. 2. Percentage of sockeye salmon at each depth fished and representative vertical temperature structure at fishing stations in the northwest (Station 2 combined with either Station 1 or 4) and southeast (Station 3) areas of the Gulf of Alaska in 1959, and the northwest area of the Gulf (Station 1 and 2) in 1960. Actual station positions are shown in Fig. 1. Percentages are based on weighted catches.

from 160 to 270 m. During this period, sockeye were caught at all five levels, down to and including 160–200 ft (49–61 m) i.e. roughly to the bottom of the thermocline. In the later period when the thermocline was much more pronounced and shallower, sockeye were caught only above it, and were apparently more vertically confined. Small catches in the southeast area during the period July 5–11 showed a similar relationship with the thermocline.

Chum Salmon (*O. keta*)

Catches of chum salmon were relatively small in 1959 and only moderate in 1960, compared with catches of sockeye (Tables I and II). The percentage of chum salmon (calculated as for sockeye) at various levels during day and night are shown in Fig. 3.

Unlike sockeye, the chum salmon catches at night, combined for all depths, were consistently larger than those during the day.

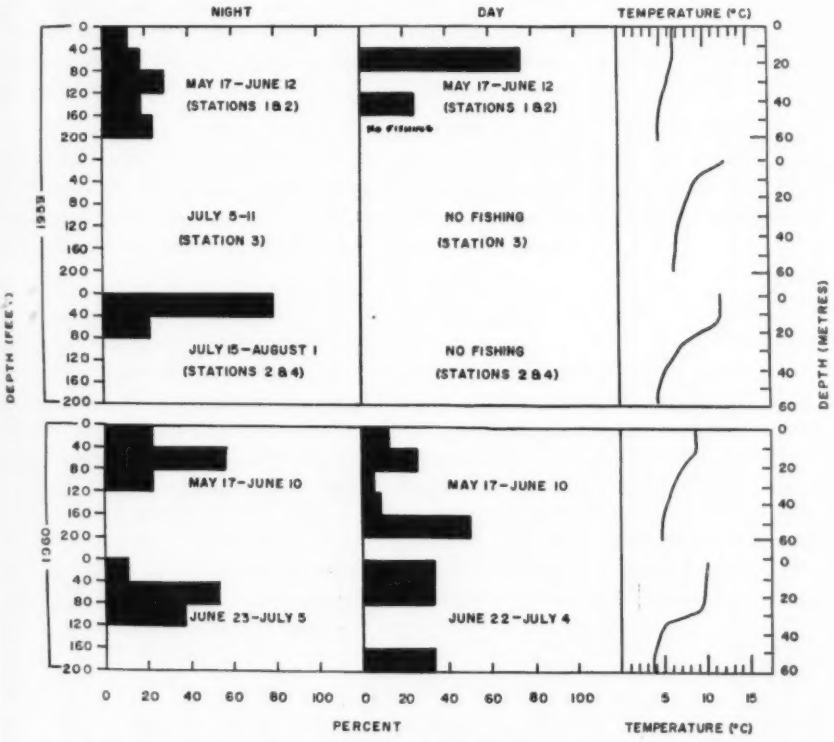


FIG. 3. Percentage of chum salmon at each depth fished and representative vertical temperature structure at fishing stations in the northwest (Station 2 combined with either Station 1 or 4) and southeast (Station 3) areas of the Gulf of Alaska in 1959, and the northwest area of the Gulf (Station 1 and 2) in 1960. Actual station positions are shown in Fig. 1. Percentages are based on weighted catches.

TABLE IV. Age composition of chum salmon caught by the surface and depth nets during the day and night in the northwest area of the Gulf of Alaska, 1960.

Period	Surface net				Depth net			
Age:	3	4	Other	Total	3	4	Other	Total
Day sets								
May 17–June 7								
No.	..	12	1	13	2	28	5	35
Percentage	..	92.3	7.7	100.0	5.7	80.0	14.3	100.0
June 22–July 4								
No.	7	15	3	25	..	3	..	3
Percentage	28.0	60.0	12.0	100.0	..	100.0	..	100.0
Night sets								
May 18–June 10								
No.	3	36	5	44	6	53	2	61
Percentage	6.8	81.8	11.4	100.0	9.8	86.9	3.3	100.0
June 23–July 5								
No.	20	19	1	40	14	7	3	24
Percentage	50.0	47.5	2.5	100.0	58.3	29.2	12.5	100.0

In the northwest Gulf (Stations 1 and 2 combined) in the early period in 1959, chum salmon were caught at night at each of the five levels fished. They were slightly more numerous at the deeper levels. Of the eight chum salmon caught in day fishing (from the surface to 160 ft) six were taken between 40–80 ft and two between 120–160 ft.

During the late part of the season, according to catches at Stations 2 and 4 combined, fishing at all levels at night produced chum salmon only from waters above 80 ft and mainly above 40 ft.

In the southeast area (Station 3) during the period July 5–11, night fishing took no chum salmon at the surface or at depth, even though sets were made down to and including the 160- to 200-ft level.

In 1960, although catches were larger than in 1959, no obvious upward shift in the vertical distribution of chum salmon was indicated as the season advanced. Through the season, and especially in the early period, fish were more concentrated nearer the surface during the night than during the day. In the late season the day catches consisted of three fish, one of which was taken at the 160- to 200-ft level.

No consistent difference in vertical distribution was apparent between 3- and 4-year-old chum salmon, the age groups mainly caught. As was the case with sockeye, older fish, presumably maturing and migrating from the high seas to coastal areas, became relatively less numerous as the season progressed, while younger fish became relatively more numerous (Table IV).

There was no conclusive evidence of any relationship between temperature conditions and vertical distribution of chum salmon during the study in these areas. In 1959 in the northwest and central areas combined, small catches in the early part of the study (May 17–June 12) did not suggest that vertical distribution, either during the day or night, was limited by temperature conditions. During the late part of the season (July 15–August 1), when fishing was conducted at night only, chum salmon were caught only above the thermocline. Fishing in the southeast area slightly earlier in the season (July 5–11), also at night, failed to catch any chums. It is notable that, in general, temperature conditions were warmer than in the northwest. In 1960, in the northwest area, no marked seasonal change in vertical distribution pattern was apparent as the thermocline developed, although the fish were closer to the surface and above the thermocline during the night.

Pink (*O. gorbuscha*) and Coho (*O. kisutch*) Salmon

Pink and coho salmon catches in 1959 and 1960 were very small (Tables I and II). In the northwest area in both years, the availability of pink salmon increased with the season.

Pink salmon were caught from the surface to the 80- to 120-ft level. Coho were caught only as deep as the 40- to 80-ft level.

DISCUSSION

Hashimoto and Maniwa (1959), on the basis of echo-sounding experiments conducted on high-seas salmon fishing grounds in the Aleutian region, stated that salmon ascended after sunset and descended after daylight, and that some were present between 30 and 50 m at all times. They also reported that strongest echoes (presumably from salmon) were concentrated in the deep-scattering layer which shifted vertically in accordance with the depth of the thermocline. Since sockeye, pink, and chum salmon are the species mainly encountered in high-seas fishing it is these species that were probably observed.

The findings from the present study are in general accord with these observations regarding the thermocline. Limited experimental depth fishing in the western Pacific Ocean and Bering Sea also provides general confirmation (International North Pacific Fisheries Commission, 1963).

Sockeye and chum salmon exhibit differences in their behaviour toward the thermocline. In the case of sockeye, particularly in the late season, the thermocline appears to present a physical barrier through which the species does not migrate, either during hours of light or darkness. Chum salmon, on the other hand, showed this reaction only during hours of darkness in the late season. Other factors therefore are presumably important in seasonal and diurnal vertical distribution of these species above the thermocline, and may include feeding behaviour, distribution of food, or other environmental features.

With evidence of a relationship between vertical migrations of sockeye and the thermocline, and with information on seasonal and regional differences in the thermal structure of the Subarctic Pacific Ocean, it is possible to speculate on the vertical distribution of the species at different places and during different seasons. According to Tully and Giovando (1962), using bathythermograph observations at Station "P" (Lat. 50°N, Long. 145°W), the thermocline begins to form in May, continues to grow and becomes shallower until September when heating ceases, and then sinks and decays. Also, Pattullo and Cochrane (MS, 1951) and Dodimead *et al.* (1963) have shown that through the summer the thermocline in general tends to become less deep from the eastern to the western regions of the Subarctic Pacific Ocean and into the Okhotsk Sea. Thus, it is conceivable sockeye during the summer may be compressed closer to the surface in the western than in the eastern region of the Subarctic Pacific Ocean. This suggests a mechanism which partially explains the tendency for sockeye density levels during this season, according to surface catches, to be higher in the western than in the eastern region (Manzer *et al.*, 1964). Later in the year and during winter, as cooling takes place and sinking of the thermocline ensues, in some areas at least the species would occur at greater depths, probably even deeper than those inhabited in May.

The catches of sockeye and chum salmon failed to reveal any differences in the vertical distribution of fish of different age-types. Since size and maturity are closely related to age it is unlikely that there are any significant differences in the vertical distribution of the immature and maturing individuals that are vulnerable to capture by the gear used. To what extent this assumption applies

to sockeye in their early ocean life is not known. Information on other fishes suggests that small, young individuals on the average do not descend to such great depths as larger individuals.

CONCLUSIONS

1. In the northwest Gulf of Alaska from about mid May to early June sockeye and chum salmon are present throughout the upper 200-ft level investigated, and may be deeper.

2. From late June through July sockeye salmon are present in the upper 120-ft level only, whereas some chum salmon are still present at least as deep as the 160- to 200-ft level.

3. From mid May through July sockeye and chum salmon ascend toward the surface during the night and descend during the day.

4. The thermocline may limit the depth to which sockeye descend, especially in late June and July. This relationship is less apparent for chum salmon. Seasonal and diurnal movements above the thermocline must be due to other factors.

5. Neither sockeye nor chum salmon, within the conditions of the experiment, showed any consistent differences in the vertical distribution between fish of different age.

ACKNOWLEDGMENTS

Doctor F. Neave, Messrs R. J. LeBrasseur, D. B. Donnelly, and G. P. Schroh individually supervised or assisted in the field program at different times. Doctors P. A. Larkin and F. Neave reviewed the manuscript and offered useful suggestions. Mr H. T. Bilton and his associates determined the ages of sockeye and chum salmon.

REFERENCES

DODIMEAD, A. J., F. FAVORITE AND T. HIRANO. 1963. Salmon of the North Pacific Ocean. Part II. Review of Oceanography of the Subarctic Pacific region. *Bull. Int. North Pacific Fish. Comm.*, No. 13, 195 pp.

DOE, L. A. E. 1955. Offshore waters of the Canadian Pacific coast. *J. Fish. Res. Bd. Canada*, **12**(1): 1–34.

HASHIMOTO, T., AND Y. MANIWA. 1959. Fish-finding on the salmon fishing grounds in the North Pacific Ocean, pages 523–524. *In* Modern fishing gear of the world. Fishing News (Books), London.

INTERNATIONAL NORTH PACIFIC FISHERIES COMMISSION. 1958. Ann. Rept. for the year 1957.
1959. Ann. Rept. for the year 1958.
1963. Ann. Rept. for the year 1961.

MANZER, J. I., T. ISHIDA, A. E. PETERSON AND M. G. HANAVAN. 1964. (In press.) Salmon of the North Pacific Ocean. Part V. Offshore distribution of salmon. *Bull. Int. North Pacific Fish. Comm.*

PATTULLO, JUNE G., AND JOHN D. COCHRANE. MS, 1951. Monthly thermal condition charts for the North Pacific Ocean. *Univ. California, Scripps Inst. Oceanogr.*, MS No. 3.

TULLY, J. P., AND L. GIOVANDO. 1963. Seasonal temperature structure in the eastern Subarctic Pacific Ocean, pp. 10–36. *In* M. J. Dunbar, [ed.] Marine distributions. The Royal Society of Canada, Spec. Publ. No. 5. University of Toronto Press.

Ocean Growth and Mortality of Pink and Chum Salmon[1]

By W. E. Ricker

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Records of length of pink and chum salmon computed from scale annuli are summarized, and are converted to show rate of growth in weight. Information is available on 11 pink stocks or groups of stocks originating at points from the Strait of Georgia to Sakhalin and Primorye, and for 7 chum stocks taken from Tillamook Bay to the Amur River and Sakhalin. Estimates of increase in weight from the time of formation of the final annulus to time of capture near shore vary from 190% to 590% for pinks maturing at age 1+, and from 60% to 92% for chums maturing at age 3+. At the end of the first year, pinks are computed to average 356 g in weight, and chums 287 g. Average instantaneous rate of growth per month in the final year is 0.28 for pinks and 0.12 for chums, each available locality being given equal weight. The seasonal distribution of growth in the final year has been estimated for pink salmon of the Bering Sea (by Birman) and for those of the central British Columbia coast (by LeBrasseur and Parker); for chum salmon an approximate seasonal distribution can be deduced from comparisons of growth rates. Combining these with the best available estimate of natural mortality (0.02 per month for salmon more than 30 cm long), calculations of net yield from high-seas fishing can be made for any desired date, and compared with the yield from a purely coastal fishery (the same escapement being provided in both cases). In all situations the catch taken on the high seas is less than that taken from the survivors of the same fish in coastal waters. The loss of yield exceeds 50% for pinks taken early in their final season, and also for chums taken early in their penultimate season.

CONTENTS

	Page
Introduction and Methods	905
Growth of Pink Salmon Stocks	908
Growth of Chum Salmon Stocks	912
Summary of Growth Rates	915
Seasonal Increase in Weight	918
Natural Mortality Rates During Pelagic Life	922
Comparisons of Growth and Mortality, and Estimates of Loss from High-Seas Fishing	926
Discussion	929
Acknowledgments	930
References	930

INTRODUCTION AND METHODS

The ocean growth and mortality of Pacific salmon has recently become a subject of live interest, especially from the point of view of assessing the effects of high-seas fishing on yield. Most work to date has concerned sockeye (*Oncorhynchus nerka*). Taguchi (1961) has considered the question for chum

[1]Received for publication June 1, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

salmon (*O. keta*), and Doi (1962a) for pink salmon (*O. gorbuscha*). The present paper summarizes growth studies on the two last-named species, and relates them to available estimates of pelagic natural mortality.

Weight–Length Relationships

Many studies have indicated that a relationship of the form:

$$w = al^b; \quad \log w = a + b \log l \tag{1}$$

describes the relationship between weight (w) and length (l) of salmon and other fish rather well. However, factors such as seasonal or diurnal variation in food present in the digestive tract, sampling difficulties, and differences in body form as between fast-growing and slow-growing fish of a particular age-group, all introduce variability; and this can make computed values of a and b imprecise and potentially misleading when fish are examined over only a portion of their total range of size. For the present purpose an overall average relationship is needed. Plots of log weight against log length for ocean-caught pinks and chums of the fingerling and the subadult size ranges, taken off British Columbia in 1955–57 by the Fisheries Research Board of Canada Biological Station (Nanaimo, B.C.), showed no significant departure from linearity, though the least-square lines fitted to the fingerlings and the subadults separately did not coincide exactly. The best value of b was close to 3.2 for both pinks and chums. LeBrasseur and Parker (1964) obtained $b = 3.25$ for pink salmon, using a wider selection of data; the final digit is of course uncertain.

The actual relationships obtained and used here are as follows:

$$\text{Pinks:} \quad \log w = \bar{3}.747 + 3.2 \log l \tag{2}$$

$$\text{Chums:} \quad \log w = \bar{3}.780 + 3.2 \log l \tag{3}$$

Here w is in grams whole weight, l is in centimeters fork length.

For comparing growth rates and mortality rates it is easiest to use the instantaneous rate of increase in weight (g) and the instantaneous rate of mortality (q), defined as:

$$g = \log_e(w_2/w_1) \tag{4}$$

$$q = -\log_e(N_2/N_1) \tag{5}$$

Here w_1 and w_2 are weights of an average fish at times 1 and 2, while N_1 and N_2 are the numbers present at those times.

Given the value of the exponent b, Kisaburo Taguchi has shown that it is not necessary to calculate actual weights in order to compute the instantaneous rate of increase in weight. Substituting (1) in (4) gives:

$$g = \log_e(al_2^b/al_1^b) = b(\log_e l_2 - \log_e l_1) \tag{6}$$

This expression is used to calculate the growth rates of Tables I–VIII, with $b = 3.2$.

Where actual weights are needed, they are calculated from (2) and (3), using the *average* lengths of successive age-groups of salmon in each locality.

Strictly speaking, because expressions (2) and (3) are based on observations of individual fish (rather than average lengths and average weights of whole age-groups) the absolute weights computed from them here should be a little too low to represent the average weight of the fish of the age-groups in question; however, the growth *rates* computed in this way are unbiased, for practical purposes.

Kinds of Growth Information

Best information on the marine growth in weight of a salmon stock would be obtained by sampling it representatively at frequent intervals. No stock has been really satisfactorily sampled, but data exist to give a fairly good idea of growth of pink salmon of the Bering Sea (Birman, 1960) and of the Fitz Hugh Sound region of central British Columbia (LeBrasseur and Parker, 1964). No comparable data have been assembled for chum salmon.

The observed increase in size of salmon tagged and recaptured has been used to estimate growth in the final year or two of life. LeBrasseur and Parker (1964) did this for pinks in their final year, and the results agreed well with the sampling method. Data for chums have not yet been summarized in this way.

Growth of a fair number of pink and chum salmon stocks has been estimated from measurements of distances between the annuli on the scales, and from the last annulus to the scale margin. Various methods have been used to convert scale measurements to fish length (Chugunova, 1959). The methods of Fraser (or Lea), of Monastyrsky, and of Segerstråle have been used in the data cited below. Trials show that the differences in the results of these methods are not sufficient to alter appreciably the growth rates obtained, particularly since we will compute rates for only the last and next-to-last growth years.

Comparison of the size of maturing Pacific salmon at two successive ages has sometimes been used as a rough measure of growth rate of the older age-group. However, it has often been demonstrated that early-maturing salmon grow more rapidly than later-maturing ones of the same year-class and sex (compare Tables V–VIII). In this situation the ratio of the sizes of maturing fish of two successive ages invariably underestimates the growth rate, usually by quite a substantial amount. Hence this paper does not use comparisons of maturing fish as means of estimating growth rate of chum salmon. The question does not arise with pink salmon, which almost all mature at the same age — 1+.

Divisions of Marine Growth

The annulus on the scale is the only widely-used criterion for dividing up the ocean growth of salmon. For pink salmon this marks the division between the first and the last *growth-years*, it being understood that both of these are shorter than 12 months. For chum salmon we will be concerned with growth in the first year (up to the first annulus), in the penultimate year (second-last annulus to last annulus), and in the final year (last annulus to scale margin). The penultimate year is here considered to be 12 months long, though it may be a little longer if the second-last annulus is formed earlier in the season than the last one. Among both chum and pink salmon, the final growth year is much shorter than 12 months: estimates are made for each stock separately in what follows.

Differences Between the Sexes

In order to avoid too extensive tabulations, and to get a more general picture, data for the two sexes combined are used in Tables I–VIII. Some authors have not recorded the sex of their fish, so their data are used as given. When growth of the two sexes has been treated separately, a simple average of the computed linear growths of the two sexes is used, giving each sex the same weight regardless of the number of fish sampled in each.

Males of *Oncorhynchus*, of all stocks examined to date, tend to grow somewhat faster than females when in the same habitat (sea or lake). Except among pink salmon, this does not necessarily mean that the males in a spawning assemblage are always of larger average size than the females. The reason is that faster-growing salmon of a given sex usually tend to mature earlier than slower-growing ones; and in addition males probably tend to mature earlier than females even apart from the average difference in growth rate between the sexes.

Obviously, if the sexes differ in abundance at each age, a combination of equal numbers of both will not be representative of the stock maturing at a particular age. It would be better to use the numbers of each sex actually sampled *if* the samples available were a random selection from the population. Unfortunately, because of marked differences between the sexes in average size and average time of migration, combined with the selectivity of at least some types of fishing gear, random sampling of a stock is probably seldom achieved; and it is rarely indeed that we *know* a sample is random in this respect. Hence for our purpose it seems better to use equal numbers of each sex, as far as the data permit.

GROWTH OF PINK SALMON STOCKS

Southern and Central British Columbia

Fraser (1920, p. 202; 1921, p. 21) gives the average standard length[2] and computed length at the annulus for pinks from Comox (middle Strait of Georgia) and Rivers Inlet (central mainland coast) in 1916, also from Deepwater Bay (Johnstone Strait) and the Fraser River in 1917. (An additional 1917 group from Pender Island were presumably mostly Fraser fish, and their growth was very similar to the latter.) Length at the annulus was calculated by assuming direct proportion between scale measurements and fish length less 41 mm (44 mm fork length) — the method initiated by Dr Fraser in 1914 (Table I). Weight increases in the final season vary from 470% to 550%.

Though much larger than the Comox fish, the Rivers Inlet pinks taken in mid July had had less time to grow in their second year than the Comox pinks, taken in late August. The Fraser River fish in 1917 were almost as large as the

[2]Fraser's standard lengths, measured to the base of the tail, have here been increased by 7.5% to convert them approximately to fork lengths. Fraser describes his method of measurement only on page 188 of the 1920 paper, where he says: "The measurements here are lower than Gilbert's, as the median caudal fin rays are included in his measurements, but are not in these". This statement is in the section on sockeye, but I have assumed (as did Gilbert, 1922) that the same procedure was used for the other species. The conversion factor of +7.5% is used by Gilbert (1922) and agrees rather well with comparative measurements made recently. The conversion is not necessary for the purpose of calculating growth rates from expression (6), but it is convenient to have the tabulated lengths all in the same unit.

TABLE I. Growth of pink salmon in British Columbia (sexes given equal weight). L_1—average computed fork length at the scale annulus: L_2—average fork length of fish when captured; g—instantaneous rate of growth in weight between annulus and margin; weight increase—percentage *increase* in weight from annulus to margin.

Place	Date of capture	No. of fish	L_1	L_2	g	Weight increase
Fraser River	Aug. 15–30, 1917	136♂ 377♀	333	588	1.82	520%
Off Comox	Aug. 15–31, 1916	256♂ 244♀	300	538	1.87	550%
Deepwater Bay	July 24–25, 1917	118♂ 63♀	319	549	1.74	470%
Rivers Inlet	mid July 1916	252♂ 248♀	330	593	1.87	550%

Rivers Inlet fish in 1916, but Fraser notes that the Rivers Inlet fish in 1917 were much larger than in 1916 — judging by bulk weights (none were measured in 1917).

CENTRAL ALEUTIANS AREA AND BERING SEA

Birman's (1960) growth data for pinks caught in 1959 south of the central Aleutian Islands are shown in Table II. The "July 10" figures represent another group of fish taken in the Bering sea at "the end of June–July" — hence probably close to the end of their growth. In addition to the growth rates (g-values) computed from lengths, those computed from Birman's "gonad-free" weights are shown. Extensive tagging along the Aleutian chain (Hartt, 1962; FRI, 1960) has shown that in recent odd-numbered years (including 1959) practically all recaptures of pink salmon tagged in this area in June have moved into the Bering Sea or in that direction; recoveries of tags in or near fresh water were mainly from the Karagin–Oliutorka–Korfa region at the base of the Kamchatka Peninsula. Though Birman's fish were taken earlier than June, there is little doubt that they too were largely from these big Kamchatka runs, so Table II

TABLE II. Growth of pink salmon sampled south of the Aleutians in late April, and a projection to July 10 on the basis of Bering Sea average sizes, from data of Birman (1960). Growth rates are estimated from lengths using expression (1), and also from the weights without gonads, given by Birman.

	South of Aleutians			Bering Sea	
	Annulus	Late April		July 10	Annulus to July 10
Fork length, *mm*	280	410		480	
Instantaneous rate of growth in weight		1.22	0.51		1.73
Increase in weight		240%	67%		460%
Weight (without gonads), g	180	643		1242	
Instantaneous rate of growth in weight		1.27	0.66		1.93
Increase in weight		260%	93%		590%

gives some idea of the amount of growth made by these pinks during their final year. The total weight increase for the season is 460% using the calculation from lengths, or 590% on the basis of Birman's weights.

Another small group of Bering Sea pinks was included in Semko's study (1939, table 14): 10 males and 10 females taken in 1929 from Korfa Bay. The weight increase from annulus to capture was 540% (Table IV), intermediate between the two figures above. Dates of capture of these fish are not given, but pinks run early in this region: the date July 15 will be used (based on the fish from the neighbouring Oliutorka region as described by Semko).

Northwestern Pacific Ocean

Hayashi (1957, table 6) gives the length at annulus of age 1+ pink salmon taken on the high seas between 145° and 173°E Long. in 1952–54. He calculated length at the annulus by Fraser's method, using 4 cm as the abscissal intercept. The lengths at capture for these fish are not given directly, but they can be calculated from the r_1 and l_1 values shown in his table using the relationship described at the foot of his page 11, with $L_0 = 4$ cm and $v/V = r_1$. In Table III lengths and computed increases in weight are shown; the latter vary from 180% to 380%.

Table III. Increase in length and weight of pink salmon taken in the northwestern Pacific Ocean. Symbols as in Table I.

Date of capture	No. of fish	L_1	L_2	g	Weight increase[a]
June 6–28, 1952	46	332	457	1.02	180%
July 12–17, 1953	17	276	408	1.24	250%
July 27–Aug. 4, 1954 (plus 4 fish taken July 9)	53	299	489	1.57	380%

[a]Not a complete growth season.

All or almost all these fish would have matured during the year of capture, but when captured their growth for the year was, in general, incomplete. The size at capture was greater in 1954 than in 1952, at least partly because the average date of capture was later. The small size of the 1953 fish corresponds with the alternation in abundance and size of pinks in Kamchatka at this period: small stock and large fish in even-numbered years, large stock and small fish in odd years.

West Kamchatka

Semko (1939, table 14) has information on growth in length of pink salmon from the regions of the Kikhchik River and the Bolshaia River (Bolsheretsk). Growth at the first annulus was computed "by the method of back calculation from the scale". Seasonal changes are examined in detail and the sexes are treated separately; here we quote only average figures for the season, with the sexes combined in equal numbers (Table IV). Computation from (6) gives

weight increases varying from 190% to 410% from annulus to capture. Semko (1939, table 27) also gives the average weights of these fish, from which growth rates can be computed that agree quite well with those in Table IV.

TABLE IV. Growth of pink salmon from 6 Asian localities. Symbols as in Table I.

Place	Date	No. of fish		L_1	L_2	g	Weight increase
Korfa Bay, Bering Sea	1929	10♂	10♀	306	546	1.85	540%
Bolshaia R., W. Kamchatka	1935	97♂	100♀	339	472	1.06	190%
Bolshaia R., W. Kamchatka	1936	101♂	97♀	298	496	1.63	410%
Kikhchik R., W. Kamchatka	1934	100♂	100♀	270	423	1.44	320%
Antonovo, W. Sakhalin	1948	...		288	463	1.52	360%
Poronai R., E. Sakhalin	1948	...		299	480	1.52	360%
Datta Bay, Primorye	1933	...		274	483	1.81	510%

Though Semko does not specify when exactly his samples were taken, information on the general course of the run is given for several regions in his table 10 and figure 7. The "maxima" of the runs used here were as follows:

Kikhchik, 1934: Aug. 2 (mid-point)
Bolshaia, 1935: Aug. 3
Bolshaia, 1936: Aug. 1

South Sakhalin

Dvinin (1952, table 6) tabulates the growth of pink salmon from Antonovo on the west coast of southern Sakhalin, and from the Poronai River emptying into Terpenie Gulf on the east coast (Table IV). Both groups increased by 360% in the final growing season. Though the date of sampling is not given, Dvinin (p. 78) says that the main run of pinks in southwestern Sakhalin is from June 15–25 to July 1–15, while in Terpenie Gulf it is July 10–20 to August 15–25 (quantifying his description as well as possible). The average is about June 29 for southwest Sakhalin and August 3 for Terpenie.

Maritime Province (Primorye)

Milovidova-Dubrovskaia (1937, table 2) gives the growth of pink salmon from Datta (or Data) Bay, which receives the Tumnin River, the largest river south of the Amur along the coast of the Maritime Province. Annulus length was calculated from scale measurements "by Einar Lea's method". In Table IV it is computed that the fish increased in weight by 510% during the final season.

Samples were taken on June 16 and on July 3, 8, and 16, 1933, though it is not stated how many of each date were used for scale reading. (The first fish entered the Tumnin during the last days of May and a few were still present in the river at the middle of August.) Here we use July 3 as a median date.

GROWTH OF CHUM SALMON STOCKS

Tillamook Bay, Oregon

Henry (1954b, table 7) computed growths of Tillamook Bay chums in length and weight, for samples taken in the year 1949. The fish were taken in the bay fishery, which in 1949 took 96% of its catch in November (Henry, 1954a), so growth can be considered complete.

The lengths quoted in Table V are simple averages of Henry's values for males and females. These fish are exceptional in that the estimated growth rate of the age 3+ group of fish in their final year was as great as in the previous year, in spite of their larger size and the shorter growing season.

Table V. Growth of chum salmon from Oregon and Washington. L_1, L_2, etc. are computed lengths in millimetres at successive annuli, the last item in each series being the observed average fork length at capture. g_2, g_3, etc. are instantaneous rates of increase in weight computed using expression (6). The last column gives the final season's increase in weight as percentage of the initial weight that season.

Age	No. of fish		L_1	g_2	L_2	g_3	L_3	g_4	L_4	g_5	L_5	Weight increase
	Tillamook Bay, 1949											
2+	12♂	3♀	305	1.61	505	0.94	678	...	...	...	...	156%
3+	128♂	129♀	300	1.59	493	0.65	604	0.65	739	...	...	92%
	Columbia River, 1914											
2+	184♂	178♀	319	1.83	565	0.80	725	...	...	...	...	123%
3+	81♂	67♀	297	1.74	512	0.79	655	0.55	777	...	...	73%
4+	4♂		282	1.75	488	0.53	585	0.48	668	0.42	762	52%

Columbia River

Marr (1943, table 2) shows the growth in length of Columbia River chums taken by gill-net and trap in the lower river. They were landed from October 13 to November 20, 1914 (Table V). Lengths of these fish were measured "with a tape over the body from the tip of the snout to the distal end of the middle caudal rays". This method gives a slightly longer measurement than the now customary procedure of laying the fish on a measuring board, but the relative picture would be practically unaffected.

Southern British Columbia

Fraser (1920) published some of the earliest data on growth of chum salmon, from catches made in the Strait of Georgia near the mouth of the Little Qualicum River and near Nanaimo. Exact dates are not given, but chums are taken only in the fall here; October 1 would be a likely average date. These fish were near the end of their migration route and had probably completed growth, for practical purposes. Fraser's lengths have been converted to fork length by increasing them by 7.5%. The fish from the two localities mentioned had very

similar growth patterns, so only the combined results are presented in Table VI, as "Lower Strait of Georgia". In addition to those shown in the table, there was 1 female chum read as age 1+, that was 532 mm in fork length and computed to be 317 mm at the edge of the first annulus.

Central British Columbia

A more northern British Columbia example has been provided by Mr H. T. Bilton of the Nanaimo Biological Station. Samples were taken in 1960 in Fishery Area No. 8 — the region of Fitz Hugh Sound and Bella Coola on the central coast. The run in this area is from early August to late September, peaking about August 20, and samples were taken proportionally to catch throughout the season. Measurements were made, on projected scale images, from the focus of the scale to the successive annuli and to the margin. An eye-fitted linear relationship between scale radius and orbit-hypural length was used to convert scale measurements to fish lengths at successive annuli. The averages of each scale measurement for all fish of each age were used, rather than measurements from individual fish. The average of the scale radii of a given age usually differed slightly from the average for fish of that length shown on the graph, so all the averages of scale measurements were adjusted proportionally before reading the corresponding length off the graph.

Table VI. Growth of chum salmon from British Columbia. Symbols as in Table V.

Age	No. of fish	L_1	g_1	L_2	g_2	L_3	g_4	L_4	g_5	L_5	Weight increase
	Lower Strait of Georgia, 1916										
2+	395♂ 379♀	307	1.76	533	0.87	700	...	...	...	...	139%
3+	767♂ 436♀	285	1.72	487	0.88	642	0.54	759	...	...	72%
4+	19♂ 3♀	282	1.67	475	0.84	617	0.55	732	0.38	825	46%
	Central British Columbia (Area 8), 1960										
2+	100	274	2.10	528	0.93	706	...	...	...	...	153%
3+	96	261	2.04	493	0.91	650	0.58	784	...	...	79%
4+	4	213	2.31	439	1.07	614	0.69	761	0.38	856	46%

Up to this point lengths were in the orbit-hypural measurement (H) — from the posterior margin of the orbit to the end of the hypural plate. These were converted to fork length (F) using a relationship established from other data for the area:

$$F = 1.308\ H - 33\ \text{mm}$$

Results are in Table VI, and also the computed rates of growth in weight.

Northwestern Pacific Ocean

Kondo and Kitahara (1962, table 7) report the growth of chums taken during 1952–54 by oceanic fishing between 180° and 155° E Long., from research vessels. Growth to successive annuli was computed from the scales. The final

year's growth on such fish is incomplete because they have not yet moved close in to the coast; indeed some of them may have been non-maturing fish.

A peculiarity of the data (Table VII) is the unusually large growth between annuli 1 and 2, and unusually small growth between annuli 2 and 3, for the age 3+ fish. The numbers are large enough that this is unlikely to be a sampling fluctuation, and typographical errors seem unlikely because it occurs in the data for each sex individually. Occurrence of false annuli on some scales might be a possibility. In contrast to age 3+, the age 2+ and 4+ chums give a growth picture consistent with what is found in samples from other regions.

TABLE VII. Growth of chum salmon taken on the high seas west of 180° Long., 1952–54. Symbols as in Table V.

Age	No. of fish		L_1	g_2	L_2	g_3	L_3	g_4	L_4	g_5	L_5	Weight increase[b]
2+	37♂	11♀	262	1.50	419	0.50	490	...	...	...	...	65%
3+	50♂	58♀	257	1.88[a]	462[a]	0.34[a]	514	0.35	574	...	...	42%
4+	1♂	10♀	224	1.50	358	0.95	482	0.58	578	0.22	619	25%

[a]These values seem irregular; see the text.
[b]Not a complete growth season.

Although Kondo and Kitahara do not supply the exact dates on which their samples were taken, they were evidently from the same cruises as the pink salmon reported by Hayashi (Table III), so the average date of capture would likely be within a week or so of July 15.

AMUR RIVER

In his study of the Amur autumn chums, Birman (1951) tabulates the growth in length of two year-classes at 3 ages of maturity, and that of age 3+ fish taken in 6 years (1925, 1932, 1946, 1947, 1948, 1949). Table VIII shows the results for the 1943 year-class at the three important ages of maturity; figures for the 1944 year-class are very similar. Table VIII also has the 6-year average for age 3+ fish, each year being given equal weight.

SOUTH SAKHALIN

Dvinin (1952, table 9) tabulates the growth of age 3+ chums from south Sakhalin in 1948: summer chums from the Khoe River (a tributary of the Poronai on the east coast — Terpenie Gulf), and autumn chums from the Tarondomari River on the west coast. Table VIII shows the data, averaged so that the sexes have equal weight. The greater growth of the Sakhalin autumn chums in their final year can be partly ascribed to a longer time spent in the ocean, but they grew somewhat faster than the summer chums in earlier years of life also.

Sampling dates are not given. The Terpenie summer run "peaks at the end of July or beginning of August", so August 1 is taken as the most probable date. For the fall chums to the rivers of the west coast, "the main part of the run is from the second half of September or the beginning of October"; October 6 will be taken as the most probable sampling date.

TABLE VIII. Growth of chum salmon from the Amur River and Sakhalin. Symbols as in Table V.

Age	No. of fish	L_1	g_2	L_2	g_3	L_3	g_4	L_4	g_5	L_5	Weight increase
	Amur River autumn chums, 1946–48 (1943 year-class)										
2+	91	280	1.78	489	0.63	595	...	...	...	...	88%
3+	296	263	1.64	439	0.81	566	0.47	655	...	...	60%
4+	150	260	1.54	421	0.73	529	0.56	630	0.39	711	48%
	Amur River autumn chums (average of 6 years)										
3+	1285	269	1.64	449	0.81	578	0.48	672	...	...	62%
	Tarondomari River autumn chums, 1948										
3+	...	291	1.33	440	0.83	571	0.61	690	...	...	84%
	Khoe River summer chums, 1948										
3+	...	255	1.60	420	0.82	543	0.49	633	...	...	63%

SUMMARY OF GROWTH RATES

PINK SALMON — FIRST YEAR

The size achieved at the annulus marking the end of the first growing season is quite varied among pink salmon (Table IX). The average for four British Columbia localities is 370 g, while for five Asian localities from west Kamchatka southward it is 271 g. This difference is large enough and the variation is small enough that it may reflect a real difference between average absolute first-year growth in weight on the two sides of the Pacific. However, more extensive sampling would be needed to demonstrate this certainly, particularly in view of large year-to-year differences among individual stocks. The largest individual first-annulus weight in the series was in fact from an Asian locality — the sparse odd-year stock of west Kamchatka in 1935.

PINK SALMON — FINAL YEAR

Table IX summarizes the instantaneous growth rates for pink salmon in the final season, from annulus to time of capture. Except for the "NW Pacific" and "Aleutians" groups, capture occurred near the end of the growing period, when the fish were close to the coast or in fresh water. Column t_2 gives the number of months from annulus (taken as January 15) to mean time of capture (in the case of river-caught fish, 6 days before capture). The average growth rate[3] for the eastern Pacific runs is 0.28 per month, and the Bering Sea samples are about the same. Asian coastal samples, from west Kamchatka southward, average 0.24 per month, while the high-seas samples average 0.22. Again these

[3]Use of an average instantaneous growth rate for the season in this section does *not* imply that this growth index remains constant throughout the growth season: available evidence suggests that it decreases somewhat from early spring onward. However, the average value of g, per month, is useful for general comparisons between stocks when the number of months involved does not differ too greatly.

TABLE IX. Summary of growth of pink salmon. L—computed average fork length in millimetres at first annulus; W—average whole weight in grams computed from the above length; g_s— instantaneous growth rate from annulus to capture; t_s—number of months from estimated time of annulus formation to time of capture (or, in some cases, to estimated time of cessation of growth); $g_s(m)$—instantaneous growth rate per month.

		First year		Final year		
	Table	L	W	g_s	t_s	$g_s(m)$
Fraser River, 1917	I	333	414	1.82	7.0	0.26
Comox, 1916	I	300	297	1.87	7.2	0.26
Deepwater Bay, 1917	I	319	363	1.74	6.3	0.28
Rivers Inlet, 1916	I	330	406	1.87	6.0	0.31
Central Aleutians, 1959	II	280	238	1.22	3.4	0.36
Bering Sea (average)	II	...	...	1.73	5.8	0.30
Korfa Bay, 1929	IV	306	318	1.85	6.0	0.31
Bolshaia River, 1935	IV	339	440	1.06	6.5	0.16
Bolshaia River, 1936	IV	298	291	1.63	6.5	0.25
Kikhchik River, 1934	IV	270	212	1.44	6.5	0.22
Antonovo, 1948	IV	288	261	1.52	5.5	0.28
Poronai River, 1948	IV	299	295	1.52	6.5	0.23
Datta Bay, 1933	IV	274	223	1.81	5.6	0.32
NW Pacific, 1952	III	332	411	1.02	4.9	0.21
NW Pacific, 1953	III	276	228	1.24	6.0	0.21
NW Pacific, 1954	III	299	295	1.57	6.4	0.25

east Pacific stocks have a somewhat greater growth rate than the west Pacific, though from their larger initial size (at the annulus) the reverse would be expected. However the data are insufficient to establish a general rule.

CHUM SALMON — FIRST YEAR

As with pink salmon, the size attained at the first annulus (Table X) among the east Pacific stocks (282 g) averages considerably more than for those of the west Pacific (237 g). However the number of stocks compared is small.

CHUM SALMON — PENULTIMATE AND FINAL YEARS

Monthly instantaneous rates of increase in weight in the penultimate year average 0.067 in the east Pacific and 0.068 in the west, with little variability (Table X). Final-year growths average 0.110 in the east Pacific and 0.128 in the west, or 0.119 overall. The smaller average rate for the east Pacific is associated with a long growing season for three of the four runs involved; the one run that matures early (Fitz Hugh Sound–Bella Coola) has an average monthly growth rate almost as rapid as the summer chums of the Khoe River. As with pinks, more samples would be needed to establish a representative picture for the two regions.

TABLE X. Summary of growth of chum salmon of age 3+ in their penultimate and final growth "years". L—computed average fork length in millimetres at first annulus; W—average whole weight in grams computed from the above length; g_3—instantaneous growth rate during the time interval between formation of the last two annuli on the scale; $g_3(m)$—monthly average instantaneous growth rate in the penultimate growth year, assuming it to be 12 months long; g_4—instantaneous growth rate from the time of the last annulus to the scale margin; t_4—estimated number of months in this interval; $g_4(m)$—monthly average instantaneous growth rate since the time of the last annulus.

		First year		Penultimate year		Final year		
	Table	L	W	g_3	$g_3(m)$	g_4	t_4	$g_4(m)$
Tillamook Bay, 1949	V	300	321	0.65	0.054	0.65	6.7	0.097
Columbia River, 1914	V	297	312	0.79	0.066	0.55	6.2	0.089
Strait of Georgia, 1916	VI	290	287	0.88	0.073	0.54	5.2	0.104
Bella Coola, 1960	VI	261	206	0.91	0.076	0.58	3.9	0.149
NW Pacific, 1952–54	VII	257	196	...	...	0.35	2.7	0.130
Amur River, 1947	VIII	269	227	0.81	0.067	0.48	4.2	0.114
Khoe River, 1948	VIII	255	191	0.82	0.068	0.49	3.2	0.153
Tarondomari River, 1948	VIII	291	292	0.83	0.069	0.61	5.4	0.113

COMPARISON OF GROWTH OF PINKS AND CHUMS

In spite of much variation between years within stocks, there is little question that pink salmon grow faster than do chums at comparable ages or sizes. Considering all the localities shown in Tables IX and X, the average weight of pinks at the first annulus is 307 g, and of chums is 258 g, giving each locality equal weight. However, the true difference in growth rates of the two species is somewhat greater than these figures suggest. Pinks form their annulus in January, on the average, but chums not until April; hence for a just comparison it would be necessary to substract whatever growth the chums make between those dates.

The same contrast is evident in comparisons within individual regions. In the lower Strait of Georgia the pinks average 356 g at the first annulus, the chums 287 g. On the central British Columbia coast, the Rivers Inlet pinks are 406 g, the nearby Fitz Hugh Sound chums 206 g. In the northwestern Pacific Ocean the pinks averaged 304 g, the chums 196 g. In the Poronai River system the pinks were 295 g, the chums 191 g. Part of the reason for the slower first-year growth of chums may be that in some Asian rivers many chums feed a while in fresh water before going to sea. However this rarely occurs in America, at any rate south of Alaska.

No very close comparison can be made of the second-year growth of the two species, because the pinks mature before the second growing season is over. However, it is clear that they grow very much faster than chums in that year, for their length when growth ceases (July or August) averages somewhat greater than that of the chums at their second annulus (the following April), in every individual locality and overall (Tables I–VIII).

Among the reasons that pinks make more rapid growth must be included the fact that in early spring they are found much farther south than most of the chums (Neave *et al.*, MS, 1963, 1964) — hence presumably have spent much of the winter in the warmer waters of more southern latitudes.

SEASONAL INCREASE IN WEIGHT

Pink Salmon

According to Birman (1960, p. 1188) pinks form their annulus very early, "not later than the first half of January", because individuals taken south of the Aleutian Islands in the second half of April, 1959, had 7 to 13 sclerites of new growth and were calculated to have increased from a length of 28 cm to 41 cm during the current year. He relates these to Bering Sea pinks taken in late June and July at an average length of 48 cm (cf. Table II).

Birman's picture of probable seasonal growth of pinks of the 1957 spawning is shown by the solid dots in Fig. 1. The date January 15 is used for average annulus formation; it is supported by 3 pinks taken by the Fisheries Research

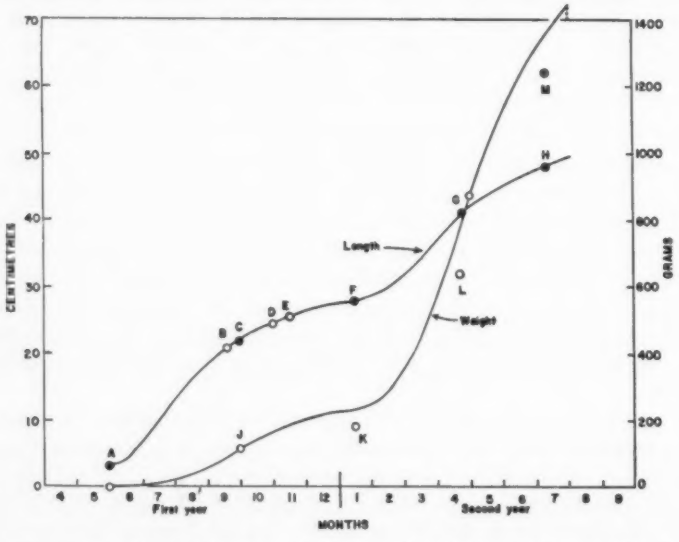


FIG. 1. Growth of pink salmon in fork length and in weight, from data of Birman (1960). Point G is the average length of pinks captured south of the Aleutian Islands in the second half of April, 1959. F represents the back-calculated length of these fish at the annulus, which is plotted at January 15. H is the average length of pinks "in the Bering Sea in late June and July", plotted on July 10. B is the average length of two pinks captured off southeastern Kamchatka in 1959. D and E are individual fish taken off southern Sakhalin, C is Birman's estimate (22 cm) of average length at the end of September, based on D and E. The smooth curve for length is drawn freehand through A C F G H. The curve for weight is derived from the length curve using expression (1). Points J, K, L, and M are Birman's figures for whole weight less gonads.

Board of Canada in the Gulf of Alaska, January 24 to February 1, 1963, which had 0, 2, and 2 sclerites of new growth, respectively (H. T. Bilton — personal communication). We have drawn a smooth curve joining these points, using 30 mm on June 1 as the average initial size. The weight curve of Fig. 1 is derived from the length curve using expression (2). Birman's weights (points J, K, L, and M) exclude the weight of the gonads; they give a very similar relative picture.

Table 13 of LeBrasseur and Parker (1964) is an estimate of the average growth in length of the 1961 year-class of pinks in the eastern Pacific, particularly those of the Fitz Hugh Sound region of central British Columbia, throughout their marine life. Interpolated and converted to weight using expression (2), final-year values are shown in column 2 of our Table XII. They differ from the Bering Sea estimates in that acceleration of growth is estimated to occur later in the year (mid April instead of mid February), and that growth ceases about 5 weeks later in the season (August 15 instead of July 10), on the average (Fig. 2). The result is that, at any given date in their final year, the central British Columbia pinks had achieved a considerably smaller fraction of their definite size[4].

Doi (1962a) used the following expression to describe the growth in weight of pinks during their last 4 months before reaching a coastal fishing site:

$$w = 2.04 - 1.04e^{-0.332t}$$

Here w = weight in kilograms; t = time in months, measured from a date 4 months before the end of growth. The fish increase in weight from 1.00 to 1.76 kg during the 4 months (Fig. 2). Doi does not state what stock or stocks this expression is derived from, or give the original data, but he applies it to the Asian region generally. The successive instantaneous monthly growth rates computed from this expression are 0.26, 0.15, 0.10, and 0.06, for a total of 0.57. It seems impossible to reconcile this quantity with the total second-year growth rates of 1.06 to 1.85 shown in Table IV (av. 1.53 for 5 localities from west Kamchatka south), because it would imply extremely fast growth during the 2 or 3 months of late winter: 0.96 from annulus formation to the start of the final 4 months of life, on the average. Pending clarification, Doi's growth picture has not been used in the computations of this paper.

Chum Salmon

Kobayashi (1959) counted the number of circuli in the marginal growth zone on chum scales caught on the high seas, and quotes earlier work by Kubo and Yamahira. Two modes were present in May. Narrow marginal zones (up to 4 or 5 circuli) were regarded as new growth for the year, while broad marginal zones (6–18 circuli) represented the previous year's growth. Kobayashi's table 5 shows that, in 1956, by June 1 practically all of the age 3+ fish had begun new scale growth, while among the age 4+ fish this was true by June 21–30. A

[4]However, the information concerning size in winter and early spring is weak, and it is possible that the two growth patterns differ much less than they appear to, apart from the difference in date of cessation of growth.

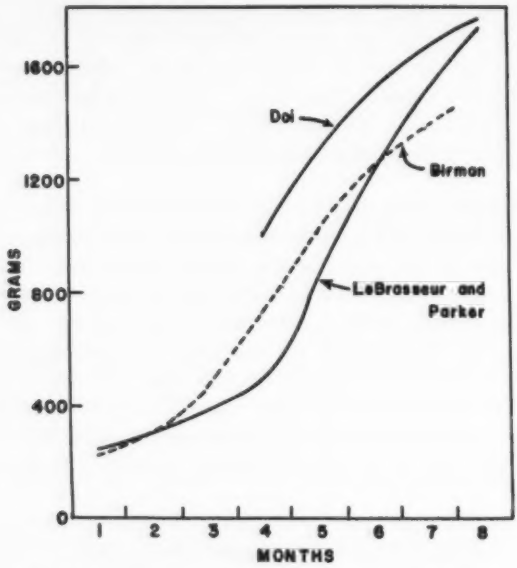


FIG. 2. Comparisons of estimates of weight increase of pink salmon in their final year, of three groups of stocks: 1. Central British Columbia, from data of LeBrasseur and Parker (1964); 2. Bering Sea, based on Birman's data (Fig. 1); 3. Doi's estimate of growth in the last 4 months of life, plotted with the end of growth at August 15.

short leftward extrapolation of a line joining the points in Kobayashi's figure 1 (omitting those after period 7, when the rate of sclerite formation falls off) suggests that the first age 3+ fish produces a recognizable circulus about April 12, and the first age 4+ fish about April 20[5].

Another published indication of the time of annulus formation in chums is by Birman (1960, p. 1190). He says that in the region south of the Aleutian Islands in the second half of April and in early May, 1959, there were many chums "which had completed 3 or 4 years, which still did not have the last annual ring; in others it was already present but without any indication of growth of the following year, and in 3 cases such growth had only just begun". (Notice that Birman evidently identifies the annulus before any new sclerites are laid down.)

Preliminary study by H. T. Bilton (personal communication) of chums caught in the Gulf of Alaska in April, 1962 and 1963, suggests a somewhat earlier average date of annulus formation than the above, apparently about April 15. In all three studies, the chums were the latest, of the species examined, to form their annulus.

[5]This indication of somewhat later annulus formation among the older fish parallels what has been found for numerous freshwater fishes.

For our purpose we will use Kobayashi's information, which suggests that age 3+ chums form their first new sclerite on April 25 on the average, while age 4+ chums do so on May 5; for age 2+ fish (not mentioned by Kobayashi) April 20 will be used. These dates are applied to Birman's data on the growth of Amur River autumn chums (Table VIII). The increase in computed weight of the three age groups of the 1944 year-class is plotted in Fig. 3. Time of cessation of growth is taken as September 1, the approximate peak of the Amur estuarine fishery for autumn chums. The absolute increase in weight from the last annulus to capture is very similar for all three age groups (1350–1640 g). The *percentage* of the final weight that is put on during the last growth year is 47% for age 2+, 37% for age 3+, and 32% for age 4+.

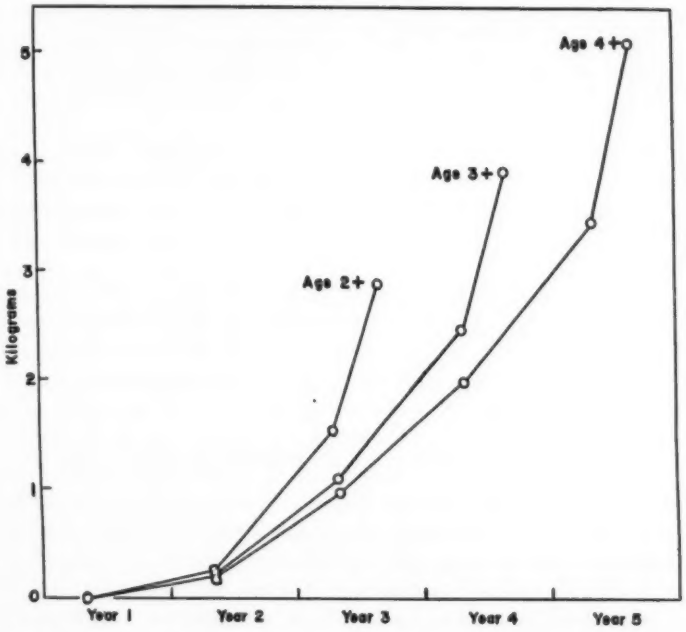


FIG. 3. Growth in weight of Amur River autumn chum salmon, computed using expression (3) from lengths obtained by back-calculation from scale reading. The lines shown merely connect the annual points, and do not represent the seasonal course of increase in weight.

There are as yet no data from tagging, or from seasonal sampling of a discrete stock, which would enable us to plot the exact trend of seasonal growth of chum salmon. However, a fairly good indication of the relative importance of the summer and winter seasons is available. The late date of annulus formation by chums implies a short growth period in the final year, all of which occurs during favorable growing weather. The average instantaneous rate of increase

in weight during this period is 0.12 per month for age 3+ fish (Table X), and no consistent geographical differences are indicated.

For the penultimate growth year (annulus to annulus), Table X shows an average total growth of 0.81, or 0.068 per month, for chums that will mature at age 3+. Comparisons of successive full-year's growth rates in Tables V–VIII, and indeed the great bulk of data on fish growth everywhere, suggest that larger fish have a smaller instantaneous growth rate in weight than do smaller fish of the same species in the same habitat — apart from seasonal changes. Hence the average rate of growth of chums during the summer months of the penultimate year must exceed the average figure 0.12 estimated for the same period in the final year. If *all* growth in the penultimate year were made during summer (say April 25 – September 30), the average monthly rate would be about 0.81/5.2 = 0.16. Hence the true average monthly summer growth rate in the penultimate year must lie in the narrow range of 0.12 to about 0.16. Taking 0.14 as the best available estimate, the total summer growth becomes $5.2 \times 0.14 = 0.73$, leaving $0.81 - 0.73 = 0.08$ for cold-weather growth made between the last two summers.

For an estimate of the distribution of summer growth within the summer season, we will not be far off if we postulate that the *absolute* increase in weight per month is constant (compare Fig. 1 for pink salmon). This means that the relative or instantaneous rate decreases throughout the summer: the appropriate figures are shown in column 2 of Table XIII.

The above division seems to be as good as anything that can be done at the moment. "Summer" growth in the penultimate year is rather unrealistically considered to end abruptly on September 30; however, if we employ a gradual phasing into the slow winter growth period, over a few weeks or months, it makes very little difference for the purpose in mind here.

NATURAL MORTALITY RATES DURING PELAGIC LIFE

Mortality and survival rate for pink and chum salmon at successive life-history stages have been summarized and interpreted by Parker (1962a), from the experimental data of Neave (1953), Hunter (1959), and others. Two estimates of "pelagic" mortality are made. The first is based on the fact that the average fecundity of the salmon in a stock determines the total mortality rate when the stock is neither increasing nor decreasing. On this basis, the total instantaneous mortality rates of the Hook Nose Creek stocks are 6.75 for pinks (which mature in their second year), and 7.15 for chums (which mature mainly in their fourth year). The difference, 0.40, can be used as a measure of the total pelagic mortality rate of chums during their two extra years of sea life, *provided* the mortality of the two species at all other stages of life is the same for these stocks. This estimate is equal to 0.017 per month.

A second method is based on survival of fin-clipped pink and chum fry at Hook Nose Creek. It requires the assumptions that the two species are equally affected by the clipping process and by the absence of both ventral fins during their later life, and that their mortality rates during coastal life in the sea are

identical. This method gives an average pelagic instantaneous mortality rate of 0.030 per month for clipped fish, which must be reduced to about 0.02 per month, or less, to apply to unmarked fish (Parker *et al.*, 1964).

Parker has discussed the reliability of these two estimates. Here we need only notice that pink fry are somewhat smaller than chum fry when they go to sea, hence should be (if anything) more vulnerable to coastal predators and more susceptible to damage during removal of fins. If there is any differential of either of these sorts, it would require *reduction* of the corresponding estimate of pelagic mortality rate. The figures obtained, 0.017 and 0.02, may be compared with an average estimate of 0.038 per month for *all* marine mortality (coastal plus pelagic) of Karluk sockeye salmon from the smolt stage onward (Ricker, 1962). The figure 0.038 includes the coastal mortality among the young fish after they go to sea at about 15 cm, hence it must substantially overestimate the true pelagic mortality rate for sockeye. Thus an estimate of 0.02 per month appears very reasonable — a little high, if anything — for losses suffered in the open sea by salmon 30 cm long and longer. This figure is also close to the natural mortality rates that have been estimated for such species as *Gadus morhua*, *Ophiodon elongatus*, *Hippoglossus stenolepis*, *Hippoglossoides platessoides*, and *Sebastes mentella*.

Parker (1962b) separates off the last two months of inshore life of pinks and chums, and assigns it a natural mortality rate of 0.07 on the basis of observations on chinook salmon in Alaska. For our purpose 2 months is too long a period of coastal mortality; tagging experiments suggest that the duration of inshore adult life of pinks and chums, up to average time of capture, must usually be about a month or a little less (e.g. DeLacy and Neave, 1947; Chatwin, 1953). Since chinook salmon differ from pinks and chums in size and habits, Parker's estimate of 0.035 per month may be too large or too small to apply to these species. For an extreme estimate we will use 0.07 *per month*, applicable in the final month prior to capture. Thus in what follows we will use two differen schedules for natural mortality in the last and (for chums) next-to-last growt years: (1) 0.02 per month throughout; and (2) 0.04 per month in all months up to the last, and 0.07 in the last month. The first of these schedules can be considered a likely average figure — the best estimate available but not the minimum possible. The second schedule is extreme, almost certainly much too large, particularly for chum salmon.

No other available estimate of natural mortality appears useful. Taguchi (1961) estimated a rather large natural mortality rate for chum salmon during the last stages of their ocean life. The method employed is similar to the one he used for sockeye, and contains a large systematic error that makes it unsuitable for this purpose (Parker, 1963).

Doi (1962b) states that "annual rate of natural mortality m is no doubt larger than 0.4 for salmon in general" (this corresponds to an instantaneous rate of $M = 0.51$); later Doi uses $M = 1.0$ as a likely average figure, or about 0.08 per month. Reference is made to an unpublished document in support of these estimates, but until the data are available there seems no point in using

TABLE XI. Computation of increase in bulk of Bering Sea pink salmon (growth less mortality) from formation of the annulus on January 15 to cessation of growth on July 10, using Birman's growth data (Fig. 1) and the two natural mortality schedules described in the text. The "Net loss" columns show the loss of commercial yield suffered when fish are harvested on the date shown, as compared with harvesting the survivors on July 10.

			Mortality schedule No. 1					Mortality schedule No. 2		
Interval limits	Weight (g)	Inst. growth rate	Inst. mortality rate	Net rate of increase	Bulk of stock	Increase yet to be made	Net loss	Inst. mortality rate	Bulk of stock	Net loss
Jan. 15	237				100	410	80%		100	77%
		0.05	0.01	0.04				0.02		
Feb. 1	250				104	406	79%		103	76%
		0.36	0.02	0.34				0.04		
Mar. 1	360				146	364	71%		142	58%
		0.48	0.02	0.46				0.04		
April 1	580				231	279	55%		220	50%
		0.41	0.02	0.39				0.04		
May 1	870				342	168	33%		319	28%
		0.26	0.02	0.24				0.04		
June 1	1130				435	75	15%		397	11%
		0.15	0.02	0.13				0.06		
July 1	1310				495	15	3%		435	2%
		0.04	0.01	0.03				0.02		
July 10	1360				510	0	0		444	0
Totals		1.75	0.12	1.63				0.26		

TABLE XII. Computation of increase in bulk of pink salmon of the central British Columbia coast, and loss from pelagic fishing. Details as in Table XI, except that the comparison is with harvesting on August 15.

			Mortality schedule No. 1					Mortality schedule No. 2		
Date	Weight (g)	Inst. growth rate	Inst. mortality rate	Net rate of increase	Bulk of stock	Increase yet to be made	Net loss	Inst. mortality rate	Bulk of stock	Net loss
Jan. 15	220				100	582	85%		100	83%
		0.16	0.01	0.15				0.02		
Feb. 1	260				116	566	83%		115	80%
		0.27	0.02	0.25				0.04		
Mar. 1	340				149	533	78%		145	75%
		0.24	0.02	0.22				0.04		
April 1	430				186	496	73%		177	69%
		0.34	0.02	0.32				0.04		
May 1	600				256	426	62%		239	59%
		0.54	0.02	0.52				0.04		
June 1	1030				431	251	37%		394	32%
		0.27	0.02	0.25				0.04		
July 1	1350				554	128	19%		496	14%
		0.18	0.02	0.16				0.06		
Aug. 1	1620				650	32	5%		559	3%
		0.06	0.01	0.05				0.03		
Aug. 15	1720				682	0	0		576	0
Totals		2.06	0.14	1.92				0.31		

the larger one even for illustration. Doi's minimum figure, approximately 0.04 per month, is the figure used in schedule No. 2, above, as an overestimate of the maximum mortality possible, on the basis of available North American data.

COMPARISONS OF GROWTH AND MORTALITY, AND ESTIMATES OF LOSS FROM HIGH-SEAS FISHING

Pink Salmon

Tables XI and XII compare the estimates of pink salmon growth for two areas with the above two mortality schedules. Also shown is the percentage loss of potential weight of landings that would be suffered if fishing were done on various dates, as compared with catching the survivors of the same fish close inshore.

The most likely times of possible high seas fishing for Bering Sea pinks would be during the period from about April 1 to June 15; for British Columbia pinks it would be April 1 to July 1. Estimates of losses from high-seas fishing are shown in columns 8 and 11 of the two tables. Using schedule No. 1, the loss among fish harvested on April 1 is 55% for Bering Sea and 73% for British Columbia, becoming less as the season advances. The difference between the two regions at a given date stems mainly from the earlier average maturity date in the more northern situation, but partly from the difference in growth patterns. Similar large estimates of loss can be obtained by applying either of the two seasonal patterns of growth in Tables XI and XII to any of the total growth increments shown in Tables I–IV[6].

The above percentage losses apply to the quantities of fish actually caught on the dates indicated, not to the total harvestable supply (defined as whatever is in excess of reproduction requirements). If a high-seas fishery takes something less than 100% of the harvestable supply, then percentage losses to the fishery as a whole are of course reduced proportionally.

One may also wish to compute percentage loss for any particular combination of poundage caught on the high seas (H) and poundage caught inshore (C), since this is the form in which catch data are available. The H pounds caught pelagically would increase to a catch of He^k pounds if the fish were allowed to proceed inshore and the survivors be taken there. Here k is the "net rate of increase" of Tables XI–XIII, summed over the appropriate time interval from the bottom of the table upward[7]. The total catch with high-seas fishing is $H + C$, and the total catch with no high-seas fishing is $He^k + C$, the same absolute escapement being allowed in both cases. Expressed as a fraction of the maximum possible catch, the loss of poundage due to high-seas fishing is:

$$\frac{(He^k + C) - (H + C)}{He^k + C} = \frac{H(e^k - 1)}{He^k + C} \qquad (7)$$

[6]Notice also that a late-autumn fishery for young-of-the-year pinks, such as exists or used to exist in one or two places along the Asiatic coast, would be very uneconomic, since the loss would exceed the 77–80% range estimated for January 15 in Table XI. The same applies to incidental capture of the young salmon anywhere, such as might occur, for example, during fall and winter herring fishing.

[7]The value of k can also be computed from the appropriate entry in the "net loss" column: $k = -\log_e(1-\text{net loss})$, net loss being expressed as a fraction.

TABLE XIII. Computation of increase in bulk of age 3+ chum salmon of average growth rate, using two different mortality schedules (see text for details). The "Net loss" columns show the loss of commercial yield suffered when fishing is done on the date shown, as compared with harvesting

TABLE XIII. Computation of increase in bulk of age 3+ chum salmon of average growth rate, using two different mortality schedules (see text for details). The "Net loss" columns show the loss of commercial yield suffered when fishing is done on the date shown, as compared with harvesting the survivors on September 1 of the final year.

		Mortality schedule No. 1					Mortality schedule No. 2			
Date	Inst. growth rate	Inst. mortality rate	Net rate of increase	Bulk of stock	Increase yet to be made	Net loss	Inst. mortality rate	Net rate of increase	Bulk of stock	Net loss
Penultimate Year										
Apr. 25				100	169	63%			100	46%
	0.04	0.00	0.04				0.01	0.03		
May 1				104	165	61%			103	45%
	0.18	0.02	0.16				0.04	0.14		
June 1				122	147	55%			119	37%
	0.15	0.02	0.13				0.04	0.11		
July 1				139	130	48%			132	30%
	0.13	0.02	0.11				0.04	0.09		
Aug. 1				155	114	42%			145	23%
	0.12	0.02	0.10				0.04	0.08		
Sep. 1				172	97	36%			157	16%
	0.11	0.02	0.09				0.04	0.07		
Oct. 1				188	81	30%			168	11%
	0.07	0.12	−0.05				0.24	−0.17		
Apr. 1				179	90	33%			142	24%
	0.01	0.02	−0.01				0.03	−0.02		
Final Year										
Apr. 25				177	92	34%			139	26%
	0.03	0.00	0.03				0.01	0.02		
May 1				182	87	32%			142	24%
	0.14	0.02	0.12				0.04	0.10		
June 1				206	63	23%			157	16%
	0.12	0.02	0.10				0.04	0.08		
July 1				227	42	16%			170	10%
	0.11	0.02	0.09				0.04	0.07		
Aug. 1				249	20	7%			183	3%
	0.10	0.02	0.08				0.07	0.03		
Sep. 1				269	0	0			188	0
Totals	1.31	0.32	0.99				0.68	0.63		

As an example, we may compare the catch without high-seas fishing with the catch when high-seas fishing takes two-thirds of the permissible weight of catch (above the fixed requirement for reproduction). High-seas fishing is considered to be centered about May 1st, and to be harvesting the central British Columbia pink salmon of Table XII, given the likely mortality schedule (No. 1). Here $H = 2C$ and $k = 0.98$. Expression (7) becomes $(2\times1.664)/(2\times2.664+1) = 0.53$, so that more than half of the potential catch is lost under these conditions. A more exact computation can easily be made for any actual fishery for which data are available showing the high-seas catch during each month (say), the procedure being to sum the coastal catches made available by refraining from pelagic fishing during each month, add the actual coastal catch, and compare the sum with the actual total catch.

Chum Salmon

Table XIII compares the estimates of average growth of age 3+ chums, described in an earlier section, with the two natural mortality schedules. The overall estimated increase in bulk of stock, using mortality schedule No. 1, is 52% in the final growth year (starting April 25 and ending August 31); and in the penultimate and final growth years together it is 169%. If fish are caught between April 25 and September 1 of the penultimate year the net loss varies from 63% to 33%. Between April 25 and August 1 in the final year, losses from pelagic fishing range from 34% down to 7% (April 1 differs very little from April 25).

Mortality schedule No. 2 suggests losses of 46% to 16% from pelagic fishing in the penultimate year (to September 1), and from 26% on down in the final year — these being underestimates. Similar calculations indicate somewhat larger percentage losses when age 2+ chums are harvested, and somewhat smaller losses for age 4+, at comparable times prior to maturity.

As an example of a computation using an extension of expression (7), consider a combination of pelagic and coastal fisheries attacking the same stock of chums. The pelagic fishery is centered on May 1st; its catch of non-maturing (but potentially age 3+), chums (H_1) amounts to 20% of the total (pelagic plus coastal) catch; its catch of maturing age 3+ chums (H_2) amounts to 60% of the total catch. The coastal catch (C) is centered on September 1 and takes maturing age 3+ fish amounting to 20% of the total catch. Here $H_1 = C$, $H_2 = 3C$; also $k_1 = 0.95$, $k_2 = 0.39$ (from Table XIII). The possible yield if all the fish were taken coastally is:

$$H_1e^{0.95} + H_2e^{0.39} + C = 8.02C$$

as compared with an actual catch of 5C. The loss is therefore 3.08/8.02 of the potential, or 38%. This is subject to the reservation that the H_1 group would become available in the coastal fishery a year later than the H_2 group, but the calculation would be correct on the average.

DISCUSSION

1. One general conclusion from the above is that growth rate considerably exceeds any reasonable estimate of mortality rate throughout the final growth year of the pink and chum salmon, the excess being greater in the case of pinks. Growth also exceeds mortality during the penultimate growth year for chum salmon. This means that a fishery that takes salmon at any time during these periods, prior to their arrival inshore, will be yielding less than an alternative fishery that took the survivors of the same fish in the inshore region. Best estimates and lower limits for these losses are given in Tables XI–XIII.

The pertinent evaluation of this loss is in absolute terms, rather than as a percentage of the total catch for a continent or region. That is, a "small" high-seas fishery that caught say 20% of the North American harvestable pinks (in excess of reproduction requirements) at a date centered on May 1, would reduce the total yield by 12%. However this would represent a loss of 26 million lb (1200 metric tons) in 1962, for example. A fairly intensive high-seas fishery, taking two-thirds of the total catch in pounds, would have meant a loss of 110 million lb from the total product taken in that year (from expression 7).

2. Of the two species considered here, the chum salmon is similar to the sockeye in characteristic age at maturity and in rate of growth during the last two growing seasons in the sea. Consequently the net increase in bulk during these seasons is similar as between the two species, as well as the losses suffered from capture on the high-seas (compare column 7 of Table XIII with the various figures on pages 539 and 540 of Ricker, 1962).

Pink salmon differ from chums and sockeye in that they grow much more rapidly during the final year, and hence increase the net bulk of their stock more rapidly, given a generally similar natural mortality rate in the final year for all three species. Consequently the loss from capturing pinks on the high-seas in the final year is greater than for chums or sockeye (compare Table XI or XII with Table XIII). On the other hand, pinks are too small to be available, during the first year, to current ocean fishing methods, so there is no loss from high-seas capture of immature pink salmon.

3. One item of potential loss from high-seas fishing is not considered in the computations of this paper: possible loss from fish being caught and removed by predators from the nets or lines, or simply from the fish falling out of the net as it is hauled up. Doi (1962a) points out that such losses may be appreciable (he considers trial values from zero up to half of the high-seas rate of fishing), but that no useful data exist concerning them. From our point of view, such losses are important if they are an *additional* source of mortality that is characteristic of high-seas fishing — that is, if inshore fisheries experience them to a lesser degree or not at all. The latter is practically true of seine fisheries, and also of the trap fisheries that were formerly common in North America but are now extinct here. Reports of predator losses for inshore gill-net fishing and trolling are common in some localities, but it is impossible to say whether they are greater or less than the corresponding losses from high-seas gill-netting or

long-lining. In any event, most pink and chum salmon in America are now taken by seines. Hence if an appreciable fall-out or predation loss does occur in association with high-seas fishing, it would to a large extent be eliminated if all harvesting were done inshore by existing methods.

4. Doi (1962a, fig. 1) has made computations of yield from different rates of high-seas fishing for pink salmon, assuming a *fixed* rate of inshore fishing. Unfortunately this assumption makes his whole presentation unrealistic, quite apart from the differences between his growth and mortality rates and those used here. A major advantage of inshore fishing is that it is very flexible, susceptible to regulation of its intensity week by week and even day by day, on individual spawning stocks or groups of stocks, so as to make possible optimum spawning escapements. Doi's figures completely fail to show this advantage obtainable by coastal harvesting, and depict instead a series of situations that are of no practical interest in North America, where close control of rate of fishing and escapement is now the rule.

ACKNOWLEDGMENTS

Cordial thanks to Mr H. T. Bilton for the data on chum salmon growth and to Mr J. I. Manzer and Mr R. J. LeBrasseur for access to field records concerning length and weight of salmon taken on the high-seas. Dr R. R. Parker read the manuscript and suggested useful changes.

REFERENCES

BIRMAN, I. B. 1951. (Qualitative characteristics of the stock and dynamics of abundance of autumn chum salmon of the Amur River.) *Izvestiia Tikhookeanskogo N.-I. Institula Morskogo Rybnogo Khoziaistva i Okeanografii* (*TINRO*), **35**: 17–31.

1960. [Times of formation of annuli on the scales of Pacific salmon, and the rate of growth of pink salmon.] *Doklady Akad. Nauk SSSR*, **132**(5): 1187–1190. (FRB Translation Series No. 327).

CHATWIN, B. M. 1953. Tagging of chum salmon in Johnstone Strait, 1945 and 1950. *Bull. Fish Res. Bd. Canada*, No. 96, 33 pp.

CHUGUNOVA, N. I. 1959. [Age and growth studies in fish.] Academy of Sciences Press, Moscow. (English version, U. S. National Science Foundation, 1963, 132 pp.)

DELACY, A. C., AND F. NEAVE. 1947. Migration of pink salmon in southern British Columbia and Washington in 1945. *Bull. Fish. Res. Bd. Canada*, No. 74, 11 pp.

DOI, TAKEYUKI. 1962a. Theoretical considerations on rationality of offshore salmon fisheries from the standpoint of effectual utilization of the population. *Bull. Tokai Fish. Res. Lab.*, No. 34, pp. 1–11.

1962b. On the problems of population dynamics relevant to immature salmons caught offshore in the North Pacific. *Ibid.*, No. 35, pp. 1–8.

DVININ, P. A. 1952. [The salmon of South Sakhalin.] *Izvestiia TINRO*, **37**: 69–108. (FRB Translation Series No. 120).

FRASER, C. McL. 1920. Growth rate in the Pacific salmon. *Trans. Royal Soc. Canada for* 1919, Sect. 5, **13**: 163–226.

1921. Further studies on the growth rate in Pacific salmon. *Contr. Canadian Biol.* for 1918–20, pp. 7–27.

FRI. 1960. Table of returns of United States tags in 1959 and 1960 (through Dec. 15, 1959). *Univ. Washington Fish. Res. Inst., Circular* No. 108–B, 10 pp.

GILBERT, C. H. 1922. The salmon of the Yukon River. *Bull. U. S. Bur. Fish.*, **38**: 317–332.

HARTT, A. C. 1962. Movement of salmon in the North Pacific Ocean and Bering Sea as determined by tagging, 1956–1958. *Bull. Int. North Pacific Fish. Comm.*, No. 6, 157 pp.

HAYASHI, SHIGEICHI. 1957. A note on the scales of pink salmon. *Bull. Tokai Fish. Res. Lab.*, No. 16, pp. 7–14.

HENRY, K. A. 1954a. Analysis of factors affecting the production of chum salmon (*Oncorhynchus keta*) in Tillamook Bay. *Fish Comm. Oregon, Contr.* No. 18, 37 pp.

1954b. Age and growth study of Tillamook Bay chum salmon (*Oncorhynchus keta*). *Ibid.*, No. 19, 28 pp.

HUNTER, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. *J. Fish. Res. Bd. Canada*, **16**: 835–886.

KOBAYASHI, T. 1959. [Age determination of chum salmon in the northern Pacific Ocean during the early parts of fishing season.] *Sci. Repts. Hokkaido Salmon Hatchery*, No. 13, pp. 1–10. (English summary).

KONDO, KEIICHI, AND MITSURU KITAHARA. 1962. A note on scales of chum salmon and of allied species. *Bull. Tokai Fish. Res. Lab.*, No. 33, pp. 1–10.

LEBRASSEUR, R. J., AND R. R. PARKER. 1964. Growth rate of central British Columbia pink salmon (*Oncorhynchus gorbuscha*). *J. Fish. Res. Bd. Canada*, **21**: 1101–1128.

MARR, J. C. 1943. Age, length and weight studies of three species of Columbia River salmon (*Oncorhynchus keta, O. gorbuscha* and *O. kisutch*). *Stanford Ichthyol. Bull.*, **2**(6): 157–197.

MILOVIDOVA-DUBROVSKAIA, N. V. 1937. [Information on the biology of and fishery for pink salmon in the Maritime Province.] *Izvestiia TINRO*, **12**: 101–114.

NEAVE, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. *J. Fish. Res. Bd. Canada*, **9**: 450–491.

NEAVE, F., J. I. MANZER, H. GODFREY AND R. J. LEBRASSEUR. MS, 1963. High-seas salmon fishing by Canadian vessels in 1962. *Fish. Res. Bd. Canada, MS Rept. (Biol.)*, No. 759, 59 pp.

MS, 1964. High-seas salmon fishing and tagging by Canadian vessels in 1963. *Ibid.*, No. 766, 38 pp.

PARKER, R. R. 1962a. A concept of the dynamics of pink salmon populations. University of British Columbia, H. R. MacMillan Lectures in Fisheries, 1960, pp. 203-211.

1962b. Estimations of ocean mortality rates for Pacific salmon (*Oncorhynchus*). *J. Fish. Res. Bd. Canada*, **19**: 561–589.

1963. On the problem of maximum yield from North Pacific sockeye salmon stocks. *Ibid.*, **20**: 1371–1396.

PARKER, R. R., E. C. BLACK AND P. A. LARKIN. 1964. Some aspects of fish marking mortality. *Intern. Comm. Northwest Atlantic Fish., Special Publ.* No. 4, pp. 117–122.

RICKER, W. E. 1962. Comparison of growth and mortality of sockeye salmon during their last two years of life. *J. Fish. Res. Bd. Canada*, **19**(4): 531–560.

SEMKO, R. S. 1939. [The Kamchatka pink salmon.] *Izvestiia TINRO*, **16**: 1–111.

TAGUCHI, KISABURO. 1961. A trial to estimate the instantaneous rate of natural mortality of adult salmon (*Oncorhynchus* sp.) and the consideration of rationality of offshore fishing. 1. For chum salmon (*Oncorhynchus keta*) 1961. *Bull. Japanese Soc. Sci. Fish.*, **27**: 963–971. (Translation by R. H. Kono).

A New Gunnel, *Pholis clemensi*, from the Coast of Western North America[1]

By Richard H. Rosenblatt[2]

Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California

ABSTRACT

A new species, *Pholis clemensi*, referred to the family Pholidae, is named and described from 12 specimens taken in southern British Columbia waters and the Strait of Juan de Fuca. *Pholis clemensi* is compared with other members of the genus, and a key is given to the North American species.

INTRODUCTION

In the spring of 1963 the author, with the aid of a grant from the H. R. MacMillan Expedition Fund of the Institute of Fisheries, University of British Columbia, undertook a survey of the fishes of the rocky subtidal of the Strait of Georgia. The major purpose of the study was to assess the effects of the peculiar hydrographic conditions of the area on the composition of the fish fauna. The recently developed collecting technique involving the use of fish toxicants and self-contained underwater breathing apparatus had been used but little, and as a result, the small fishes of the rocky subtidal were rather poorly known (Rosenblatt and Wilkie, 1963; Wilkie, 1963). One of the by-products of this study was the capture of 11 specimens of an eel-blenny which proved to be an undescribed species of the genus *Pholis*. The species is here described as *P. clemensi*.

It is a privilege to name this species in honour of the late Dr W. A. Clemens, in recognition of his contributions to ichthyology, and especially of his works on the fishes of western Canada.

METHODS

Vertebral counts were made from X-ray negatives. Measurements were made with needle-point dial calipers or flat-point dividers. The terms used are those of Hubbs and Lagler (1958), with the following exceptions.

Vertebrae. In the Pholidae there is no haemal spine, instead the parapophyses unite to form the so-called haemonephrapophyses (Makushok, 1958). The vertebra following the first interhaemal was therefore considered to be the first caudal vertebra.

[1]Received for publication August 4, 1964.

[2]Contribution from the Scripps Institution of Oceanography, University of California, San Diego, and the Institute of Fisheries, the University of British Columbia.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

TABLE I. Counts, and measurements in millimeters, of the holotype and paratypes of *Pholis clemensi*.

Collection:	BC 63-910					BC 63-934			BC 63-938		BC 63-938	UMMZ 135893
Sex:	♂	♀	♀	♀?		♀	♂	♂	♂	♂		
Standard length	115.5	140	73	67.5	32	104.6	93.0	88.0	95.5	76.6	61	71.5
Pre-anal length	53.0	63.7	33.6	31.9	–	47.4	43.4	41.3	44.4	37.4	–	35.4
Urosome length	63.4	78.5	38.7	35.0	–	56.7	50.5	48.0	51.5	40.9	–	37.4
Head length	11.9	13.2	8.4	7.5	–	11.4	10.0	7.9	10.4	8.1	–	8.5
Occiput-isthmus	7.2	7.5	5.0	4.7	–	6.6	6.0	5.0	6.4	5.8	–	–
Eye length	2.5	2.8	1.9	1.9	–	2.5	2.1	1.9	2.2	2.0	–	1.9
Snout length	2.1	2.9	1.5	1.4	–	2.1	1.9	1.6	1.9	1.6	–	1.8
Upper jaw length	3.5	3.6	2.0	2.1	–	2.9	2.5	2.5	2.9	2.4	–	2.4
Body depth at:												
Pelvics	8.4	9.4	5.7	5.3	–	8.4	7.3	6.9	7.5	6.5	–	–
Anus	11.5	12.0	5.6	5.0	–	8.0	8.4	7.0	8.4	6.9	–	5.6
Caudal base	3.4	3.9	2.5	2.1	–	3.3	3.0	3.0	3.0	2.9	–	2.4
Pectoral length	6.0	6.0	4.0	3.7	–	4.9	4.0	4.1	4.9	4.9	–	4.4
Mid-caudal ray length	8.6	9.9	5.7	5.0	–	–	6.8	6.4	7.4	6.5	–	6.4
Dorsal spines	LXXXIX	LXXXIX	LXXXIX	LXXXIX	LXXXVIII	LXXXVII	LXXVIII	LXXXVIII	LXXXIX	LXXXVII	XC	LXXXVII
Anal rays	II, 52	II, 52	II, 51	II, 52	II, 53	II, 52	II, 51	II, 52	II, 51	II, 52	II, 52	II, 50
Pectoral rays	14–14	13–13	13–13	14–?	–	13–?	13–13	14–14	13–13	14–14	14–14	13–13
Pelvic rays	I, 1	I, 1	I, 1	I, 1	I, 1	I, 1	I, 1	I, 1	I, 1	I, 1	I, 1	I, 1
Caudal rays	7+8	7+7	7+6	6+6	6+6	7+7	7+7	7+6	8+7	6+7	6+6	7+6
Vertebrae	37+59	38+57	38+58	37+59	–	37+59	39+59	38+58	38+58	38+57	38+59	37+57

CAUDAL RAYS. As pointed out by Makushok, the rounded shape of the caudal and the branching of the accessory rays make it impossible to give an accurate external count of the principal caudal rays. In my material however, I found it extremely difficult to determine accurately from radiographs the number of rays actually articulating with the urostylar hypurals. The count given is therefore the total number of branched rays.

ANAL RAYS. None of the anal rays is branched, and the last two are borne on separate basals. The count given is therefore the total count.

UROSOME. This was measured as the distance from the anal origin to the mid-base of the caudal.

DESCRIPTION

Pholis clemensi n. sp.

The following description is based on all the specimens. The first number is the mean, followed by the range in parentheses. The type agrees with the general description except where otherwise noted. Counts and measurements of the type and individual paratypes are given in Table I.

Dorsal spines 88.3 (87–90); anal II, 51.7 (II, 50–53); pectoral 13.4 (13–14); pelvic I, 1; branched caudal rays 13.3 (12–15); total vertebrae 96.1 (95–98); precaudal vertebrae 37.7 (37–39); caudal vertebrae 58.4 (57–59).

Body elongate, laterally compressed, greatest depth about one-eleventh or one-twelfth of standard length. A groove along lower side, running from pectoral base back to anus, separating belly from lower side. Head one-eighth to one-ninth of standard length. Eye placed high on head, but not entering outline of top of head. Eye length slightly greater than snout length, 4.3–4.7 in head length. Snout blunt and steep, slightly inflated in profile. Mouth strongly oblique, lower jaw ending at or slightly above level of lower margin of pupil. Maxillary extending back to a point opposite anterior margin of orbit. Upper lip as a broad fold continuous across snout, lower lip with a median frenum. Single nostril opening in a short tube equidistant from edge of upper lip and anterior-margin of eye.

Head pores of lateral line system large, but few in number. Two nasal pores, five suborbital pores, and normally six (on the right side of the type the middle two are missing) postorbital pores. Three occipital pores, five preopercular pores, and four mandibular pores in all specimens.

Teeth strong, bluntly conical, and slightly recurved. Teeth in both jaws in two rows anteriorly and one row posteriorly. Inner row better developed in upper jaw. Three to five teeth, similar to jaw teeth but smaller, on head of vomer (these teeth are difficult to see, because of presence of numerous papillae on roof of mouth). No teeth on shaft of vomer or on palatines. Tongue short and blunt, not forming much of floor of mouth.

Gill membranes united, but free from isthmus. Gill arches examined in the 104-mm paratype from BC 63-910. Four gill arches, with a restricted slit behind last. Gill-rakers on first arch 11, stout but pointed, length about one-half of pupil diameter. Pseudobranch present, with 5 thick, heavy lamellae. First gill slit restricted dorsally by a membrane, similar in shape and texture to oral valve.

Scales very small but partially imbricated, present on entire body, but lacking on head and fins.

Males with a slender, fingerlike penis inside a prominent tube formed by a raised skin-fold surrounding urogenital area. In the female, edges of anus and urogenital opening are plicated.

Dorsal and anal fins connected to caudal. Dorsal connected to caudal to full height of last spine, but ventrally there is a slight notch between anal and caudal. Dorsal spines all pungent, short, and with tips strongly hooked backward. Dorsal covered with thick skin, so that only the tips of the spines protrude. Anal spines likewise embedded in a thick sheath. Skin over soft anal relatively thin. Pelvics covered with skin, the spine thick and sharp, its length about equal to the snout.

The colors, which in life were shades of magenta and silver, faded in alcohol to tones of brown and tan. The basic pattern is of mottlings on the sides, but there is much individual variation. In most of the specimens, there is a tendency for alternating light and dark areas to form a series of chain-like markings along the lower sides. In some, however, the dark areas are broadly confluent ventrally and surround a series of light spots.

Along the upper sides there is a series of dark marks, each followed by a light area which contains a few large melanophores. There is a series of 13–15 dark marks along the dorsal fin. These vary from round dots (as in the type) to squarish blotches and may be surrounded, or followed, by a light area. The other fins are plain-colored, being either clear or slightly dusky.

Head darker above; snout and lower parts of operculum light. A light mark (silver in life) with dark borders runs back from eye. An ill-defined dark mark beneath eye. Underparts of head dusky, but with light areas across throat and just behind posterior ends of the maxillae.

Some of the specimens differ in being appreciably paler. The basic pattern is, however, the same. The difference does not seem to be related to habitat, since it involves specimens taken at the same time and in the same general habitat. The 32-mm juvenile is quite pale, and appears almost colorless. Under magnification it is seen, however, that the adult color pattern is already outlined. In addition there is a series of black punctuations running from the middle of the pectoral base to the anus, another along the ventral mid-line, and a black dot at the base of each anal ray. These are no doubt remnants of the post-larval color pattern.

IDENTIFICATION

The species of *Pholis* have not been revised recently. However, Makushok (1958) in his review of the northern blennioids has diagnosed the family Pholidae and the genus *Pholis*, and brought together meristic data for the species. It is clear from these data that *P. clemensi* is distinct. In addition, specimens of *clemensi* have been compared with material of *P. gunnellus*, *dolichogaster*, *laeta*, *ornata*, and *schultzi*, the last three of which occur in the same geographic area.

Pholis clemensi may immediately be distinguished from all its cogeners by the number of dorsal and anal rays. The only other species of *Pholis* which has as many as 50 anal soft-rays is *P. dolichogaster* (48–51), but in that species there are 93–96 dorsal spines rather than 87–90.

In addition *P. clemensi* may be distinguished from all other species of the genus except *P. fangi* by the relative length of the urosome. In *P. clemensi* and *P. fangi* the distance from the anal origin to the caudal midbase exceeds the distance from the anal origin to the tip of the snout. In *P. clemensi* the urosome exceeds the preanal by one-half to three-quarters of a head length, and in *P. fangi* it is longer by about the length of the snout (taken from the figure of the type given by Wang and Wang, 1935). In all other species of *Pholis* (in fact in all other pholids) the urosome length, when projected forward, falls short of the rear of the head.

FIG. 1. Holotype of *Pholis clemensi*, a 116.5-mm male, BC 63 910.

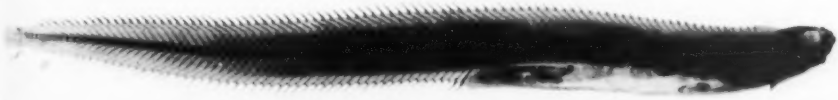


FIG. 2. Radiograph of holotype of *Pholis clemensi*.

Pholis clemensi and the Asiatic *P. fangi* do not, however, appear to be very close. The type of *fangi* has 78 dorsal spines (87–90 in *clemensi*), 39 anal soft-rays (50–53 in *clemensi*), the pectoral equal to the head length (rather than one-half the head length), and scales on the head (head naked in *clemensi*).

In order to facilitate the identification of *P. clemensi*, the following tentative key to the species of *Pholis* of western North America was prepared:

1a. Dorsal spines 74–79. A series of dark marks and light interspaces separated by dark borders, along dorsal base.

2a. Borders of light oval-shaped marks along dorsal base shaped as (), but often becoming indistinct or more or less vertical posteriorly.

Pholis laeta (Cope)
(Bering Sea to N. California)

2b. Borders of wedge-shaped light areas along dorsal base shaped as /\ or)(.

Pholis ornata (Girard)
(British Columbia to N. California)

1b. Dorsal spines 80–96. Dorsal base colored like sides, or with a series of dark spots along dorsal fin, which encroach on dorsal base.

3a. Dorsal spines 93–96. *Pholis dolichogaster* (Pallas)
(Japan to Bering Sea)

3b. Dorsal spines 80–90.

4a. Anal origin closer to tip of snout than caudal mid-base by a distance equal to at least the postorbital head length. Anal soft-rays 50–53.

Pholis clemensi n. sp.
(Straits of Georgia and Juan de Fuca)

4b. Anal origin closer to caudal mid-base than tip of snout. Anal soft-rays 40–44.

5a. Sides with a series of 10 white blotches along dorsal base, and a series of irregular white parallel bars ventrally. A white bar extending from occiput to isthmus through and behind eye.

Pholis gilli Evermann and Goldsborough
(Bering Sea)

5b. Sides mottled with light and dark areas, but no prominent white blotches and bars. A light area extending down and back from lower margin of orbit. Anal usually barred.

Pholis schultzi Hubbs in Schultz
(Washington to N. California)

ECOLOGY

The British Columbia specimens of *P. clemensi* were taken among rocks in from 40–90 ft (12–28 m) of water. The water at these depths was clear, cold (48–51°F; 8.8–10.5°C) and of relatively high salinity (ca. 28‰). The water in the upper 25 ft (8 m) in inshore localities in the Strait of Georgia is very different at that time of year (June). It was warm (58–61°F; 14.4–16°C), of low salinity (ca. 18‰), and extremely turbid due to river run-off. At all of the stations except the deepest, there was much algae. The specimen from Protection

Island, Washington, was dredged in 180 ft (55 m), presumably among rocks. The available evidence indicates that *P. clemensi* is an inhabitant of moderate depths. It is likely that its horizontal range will be found to be more extensive when more collections are made in suitable habitat at moderate depths.

REMARKS

When it was first examined, there was some doubt as to the familial and generic affinities of this species. The relative length of the anal base was puzzling since in all American pholids the anal is short-based, and all stichaeids have a long anal base (Wilimovsky, 1958, p. 13). However, certain internal characters indicate that *P. clemensi* belongs in the Pholidae. Among these are the absence of ribs, the presence of haemonephrapophyses (unique to the Pholidae), the asymmetry of the vertebrae, and the absence of pyloric caeca. Within the Pholidae, the presence of two anal spines, the correspondence of interhaemals and haemal spines at the beginning of the anal, and the presence of pelvics with one spine and one soft-ray, indicate placement in *Pholis*.

MATERIAL

HOLOTYPE. Fish Collection, Institute of Fisheries, University of British Columbia, *BC 63-910*. S. E. side Bowyer Island, Howe Sound, British Columbia; depth, 30–45 ft (9–12 m), surface temperature, 62°F (16.6°C); bottom temperature, 49°F (9.4°C); bottom, rocks over fine sand; collectors, R. Rosenblatt, D. Creed, T. Carefoot; June 13, 1963.

PARATYPES. *BC 63-910*. From the same collection and bearing the same data as the holotype. *BC 63-934*: Martin Island, Pender Harbour, Malaspina St., B.C.; depth, 25–50 ft (8–15 m), surface temperature, 59.5°F (15.4°C); bottom temperature, 49°F (9.4°C); vegetation: some *Laminaria* at 25 ft (8 m), blue, green, and red algae below; June 10, 1963. *BC 63-938*: Pearson Island, at mouth of Pender Harbour; depth 85–100 ft (26–31 m); bottom — rock, sand, and fine sediment; June 12, 1963. *BC 63-939*: Martin Island, Pender Harbour; depth, 35–50 ft (11–15 m); bottom temperature, 50°F (10°C); bottom — large rocks, fine shell, and sand; June 1963. University of Michigan, Museum of Zoology, *UMMZ 25258*: Protection Island, Strait of Juan de Fuca, Washington; dredged in 180 ft (55 m); April 13, 1941.

ACKNOWLEDGMENTS

The material on which this study is based was collected with financial aid from the H. R. MacMillan Expedition Fund. The illustration was drawn by Mrs Gladys Clawson. Drs C. L. Hubbs and Arthur Welander had recognized the distinctiveness of the UMMZ specimen, and were intending to describe it as part of a long-term study of the genus *Pholis*. They kindly turned it over to me for inclusion in this paper. I would also like to thank Messrs Kenneth Stewart and Donald Wilkie, who introduced me to the rigors of diving in boreal waters.

REFERENCES

EVERMANN, B. W., AND E. L. GOLDSBOROUGH. 1907. The fishes of Alaska. *Bull. Bur. Fish.*, **26**: 219–360.

HUBBS, C. L., AND K. F. LAGLER. 1958. Fishes of the Great Lakes region. *Bull. Cranbrook Inst. Sci.*, No. 26, 213 pp.

MAKUSHOK, V. M. 1958. The morphology and classification of the northern blennioid fishes. *Trudy Zool. Inst. Akad. Nauk SSSR*, **25**: 3–129. [Russian original and translation by Alice R. Gosline distributed by Division of Fishes, U.S. National Museum, 1959.]

ROSENBLATT, R. H., AND D. W. WILKIE. 1963. A redescription of the rare cottid fish, *Artedius meanyi*, new to the fauna of British Columbia. *J. Fish. Res. Bd. Canada*, **20**(6): 1505–1511.

SCHULTZ, L. P., AND C. L. HUBBS. 1961. Early nomenclatural history of the nominal cyprinid genus *Oregonichthys* and the blennioid *Pholis schultzi*, fishes of western North America. *Copeia* No. 4: 477–478.

WANG, K. F., AND S. C. WANG. 1935. Study of the teleost fishes of coastal region of Shangtung III. *Science Soc. China, Contr. Biol. Lab., Zool. Ser.* **11**(6): 165–237.

WILIMOVSKY, N. J. 1958. Provisional keys to the fishes of Alaska. U.S. Fish and Wildlife Serv. Fish. Res. Lab., Juneau, Alaska.

WILKIE, D. W. 1963. Occurrence of the longfin sculpin, *Jordania zonope* Starks 1895, in British Columbia. *Copeia* 1963 (3): 588–590.

Oceanographic Regions and Assessment of Temperature Structure in the Seasonal Zone of the North Pacific Ocean[1]

By John P. Tully

Fisheries Research Board of Canada
Pacific Oceanographic Group, Nanaimo, B.C.

ABSTRACT

There are eight climatic regions from the Equator to the Arctic in the Pacific Ocean. In each region the distinct oceanographic temperature structures and their seasonal sequences are described and related to surface weather processes and transport. Procedures for observation and interpretation of data must be adapted to suit the regional models of structure and behaviour. However, a rational universal system of information presentation is feasible and is demonstrated. The concepts may be extended to other oceans.

CONTENTS

	Page
Processes and Structures	942
Transport	943
Heating and cooling	945
Precipitation and evaporation	945
Mixing	945
Internal waves	950
Regions	951
Tropical Region (Tropics)	951
Subtropic Region (Subtropic)	953
Subarctic Region (Subarctic)	954
Pacific Arctic Region (Arctic)	956
Transport Regions	957
Kuroshio	957
Oyashio	958
Confluence Region	958
Domains	959
Coastal Region	959
Charting Temperature Structure	960
Conclusions	969
References	969

Since 1958 the federal naval and fisheries agencies in the United States and Canada have undertaken to create oceanographic information services, modelled on the concepts of the national Weather Services. The object is to assemble temperature data by radio aud present the significant features of structure quickly, while they still exist, in chart forms which can be broadcoast by radiofacsimile techniques, to provide the basis for assessment and forecasting the oceanographic (temperature) situations.

[1]Received for publication April 21, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

At present there are several types of presentations, each based on familiarity with local regions of interest. However, when these procedures are extended to other oceanographic regions their inadequacy becomes apparent. A universally meaningful and usable presentation is required.

Such procedures have been established in the Weather Services for many years. The data content and format of the standard weather charts are the same in all parts of the world. However, the interpretation of the data is determined by regional or local weather patterns and behaviour.

The present study was undertaken to demonstrate that a similar philosophy is feasible in oceanography. This requires definition of the principal oceanographic regions in at least one quadrant of the World Ocean (the North Pacific); definition of the significant features or structure[2] and behaviour of at least one property (temperature); and definition of suitable forms of data presentation.

To fulfil these requirements, the oceanographic structures (Fig. 1) north of the Equator in the Pacific Ocean have been examined to define regional oceano-

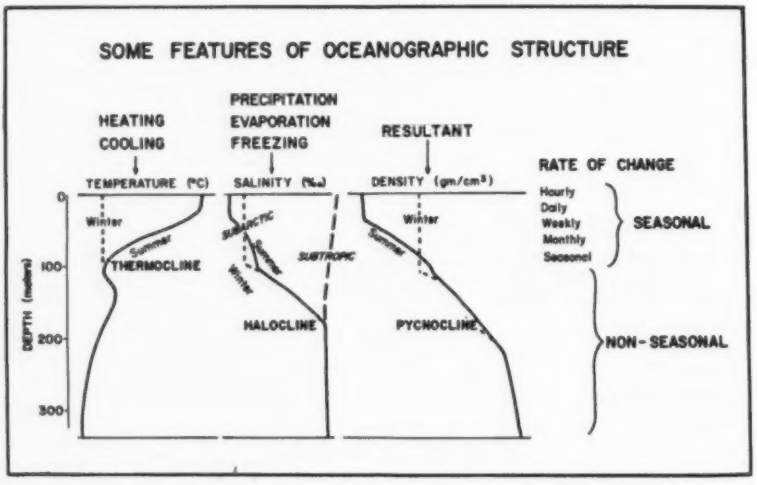


FIG. 1. Oceanographic structure general.

graphic characteristics and behaviour that can be used as rational bases for assessment and forecasting temperature structure.

PROCESSES AND STRUCTURES

The properties of sea water are changed by surface processes such as heating, cooling, precipitation, evaporation, and freezing which are functions of atmos-

[2]Following the usage of Tully and Barber (1960), Dodimead (1961), and others, the term "structure" is used here to signify the distribution (concentration, etc.) of a property with depth. Horizontal structure signifies the distribution with distance. The term is used in contrast to "profile", etc., which signify the characteristics of graphs of the distributions.

pheric weather, latitude, and season. The surface waters may be mixed downward by wind action or convection. The response diminishes and the lag increases with depth so that the effect of local surface processes vanishes at some depth, usually between 100 and 200 m. The principal structures in this *seasonal zone*[3] are a surface mixed layer, a seasonal thermocline, and/or a halocline whose occurrence, magnitude, and behaviour are consequences of the surface processes. Hence, the structure in the seasonal zone is variable and must be examined continually.

In the deep water, below the seasonal zone, the changes of structure are small, non-seasonal, and usually can be assessed from accumulated historical data and catalogued in any suitable manner. They need not be considered further here.

Within the seasonal zone, it may be realized that oceanographic structures will become wholly adjusted to the local surface processes if the waters remain long enough in one climatic region. In general, the surface processes vary with latitude. Hence, the nature of ocean transport is a primary consideration.

Transport

Figure 2 shows the major surface circulation in the North Pacific Ocean. The volume transport is the same between each pair of lines. Where the lines are close together the flow is rapid. Where the spacing is wide the flow is slow.

[3]Following the usage of Tully (1949), Doe (1955), and others, the term "zone" is used to signify a layer or thickness which encompasses some (defined) feature of structure, property or behaviour in the sea. This term is more specific than "layer" which is used variously to designate strata of any order.

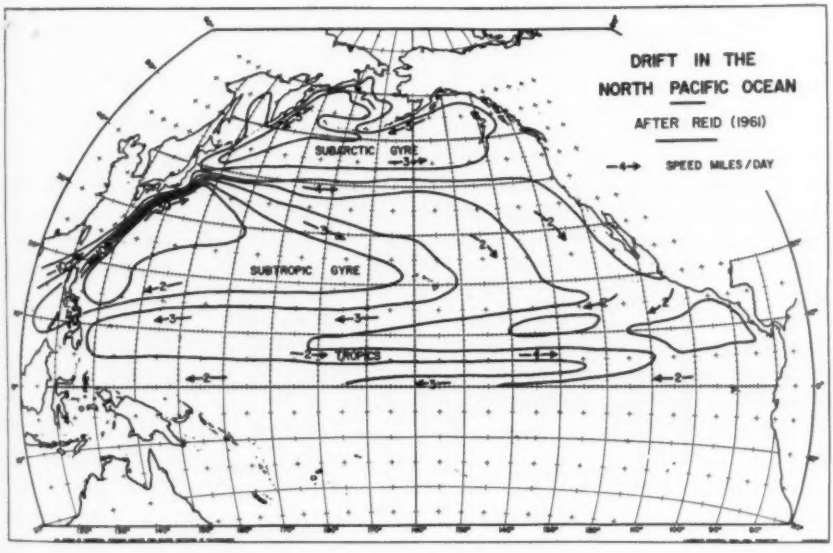


Fig. 2. Drift in the North Pacific Ocean.

The principal features are several zonal flows in the tropics, a cyclonic gyre in the subtropics and an anti-cyclonic gyre in the subarctic. The centers of rotation of these gyres are displaced far to the westward.

In the central part of the ocean, at all latitudes the flow is primarily zonal and slow (2–4 miles/day) so that the waters remain in constant climatic conditions for many months. They become adjusted to the surface processes throughout the seasonal zone.

In the eastern part of the ocean the flows become meridional but remain slow (2–4 miles/day). To some degree the waters retain their properties, but on the whole they tend to adjust to the changing climate en route.

Along the western boundary the flows (25–70 miles/day) are too rapid to permit adjustment of the waters to the changing climate. These are transport regions. Finally, there is a region of confluence, off northern Japan, where the boundary flows meet and turn eastward to form the West Wind Drift.

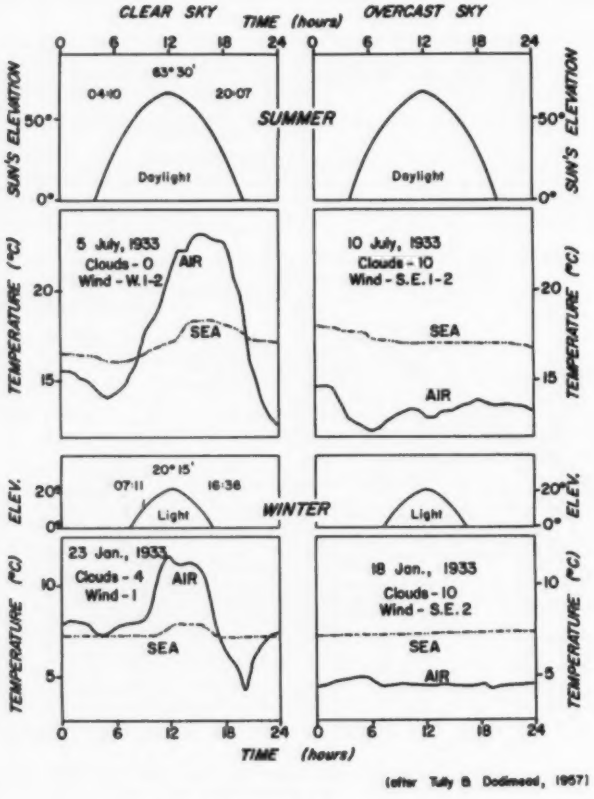


FIG. 3. Diurnal heating and cooling.

Heating and Cooling

The sea is essentially a black body which absorbs about 95% of all solar energy and radiates heat (von Arx, 1962). Heating occurs only during daytime and varies with the sun's altitude (latitude and date) and cloud cover. Cooling is due to evaporation, back radiation, and conduction from the sea surface and is continuous by day and night. Hence (Fig. 3) there may be heating or cooling during daytime, depending on which process is dominant, but invariably the sea cools by night. In consequence there is a diurnal cycle of heating and cooling which leads to changes in the near surface temperature structure. This cyclic change is sometimes called "afternoon effect".

During the heating season, when the sun is north of the Equator, the daytime heat gains in the northern oceans exceed the nighttime heat losses. Heat accumulates in the sea and the temperature increases to the end of the heating season (Fig. 4). Conversely, during the cooling season, when the sun is south of the Equator, there is a net loss of heat. Thus the sea integrates the daily heating and cooling cycles into an annual temperature cycle in which the surface waters are warmest in early September and coldest in late March.

As shown in Fig. 5, the surface waters are warmest near the Equator (28–30°C) and coldest in the Arctic, where ice is formed during the winter. Between these extremes the temperature is approximately a function of latitude, except in the boundary regions.

The seasonal range of temperature (Fig. 6) is near zero in the tropics signifying that there is no seasonal cycle. It increases northward to a maximum (9 C°) in mid latitudes and then decreases very slightly (6 C°) through the subarctic. In the Bering and Okhotsk Seas in the northwestern ocean the annual temperature range straddles the freezing point. In those areas ice is formed during the winter. Hence, by definition they are Arctic, although their circulation is part of the Subarctic Gyre.

Precipitation and Evaporation

Precipitation and evaporation have a marked effect on the salt content stability of the near-surface waters. Figure 7 shows that in the tropics there is excess precipitation at the western and eastern limits of the ocean, and a near balance in the middle. There is excess evaporation in the subtropics and excess precipitation in the subarctic and arctic.

Mixing

Heating and cooling, precipitation and evaporation occur at the sea surface. Then the surface waters are mixed downward by wind or convection forming a homogeneous layer (Fig. 1) whose depth is appreciable and varies seasonally. Below this there are gradients (clines) in the structure separating the surface dominated waters from the underlying waters.

Consider the mixing processes. There is a frictional transfer of wind energy to the sea which causes transport. Also, it causes waves and internal turbulence which result in local mixing. This downward transfer of energy is opposed by internal friction (viscosity) in the water. Thus the turbulence (mixing) de-

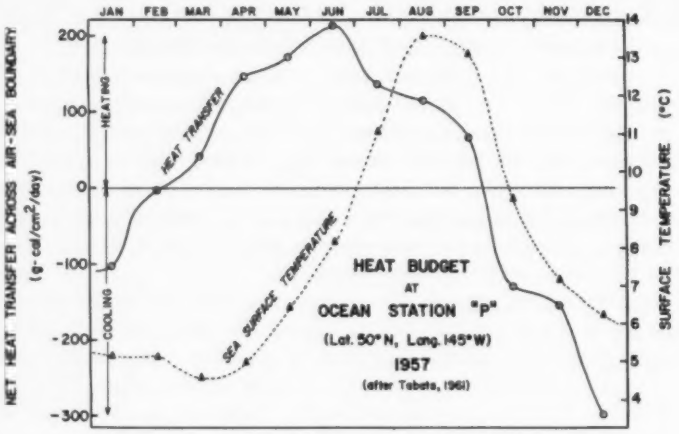


FIG. 4. Seasonal cycle of heating and cooling.

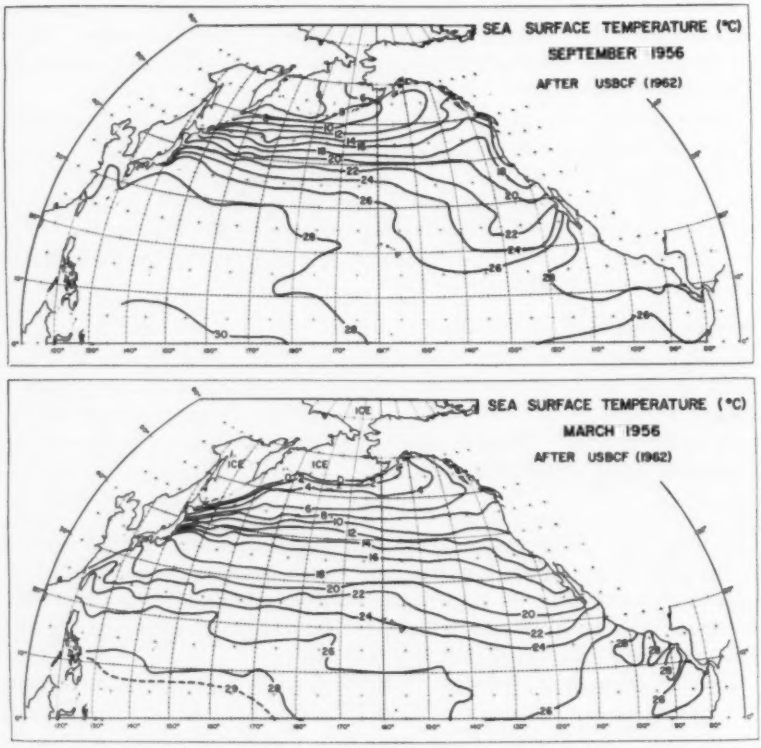


FIG. 5. Surface temperature.

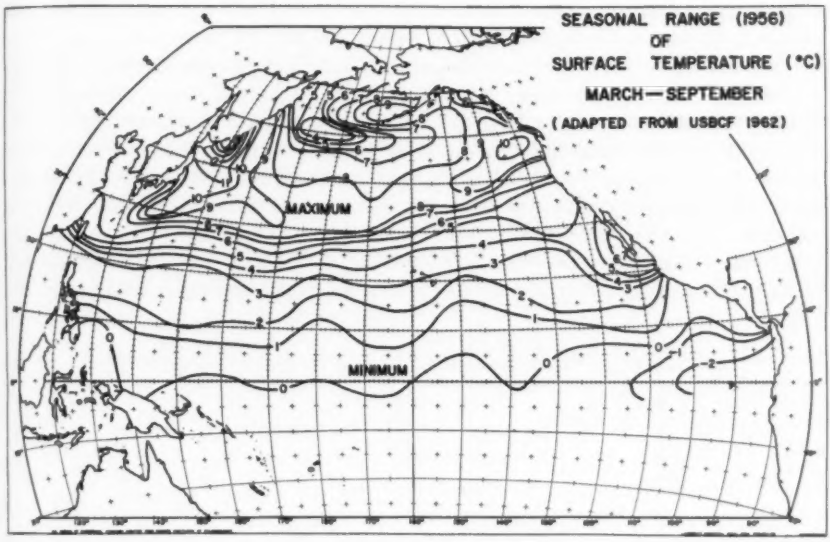


FIG. 6. Seasonal range of temperature.

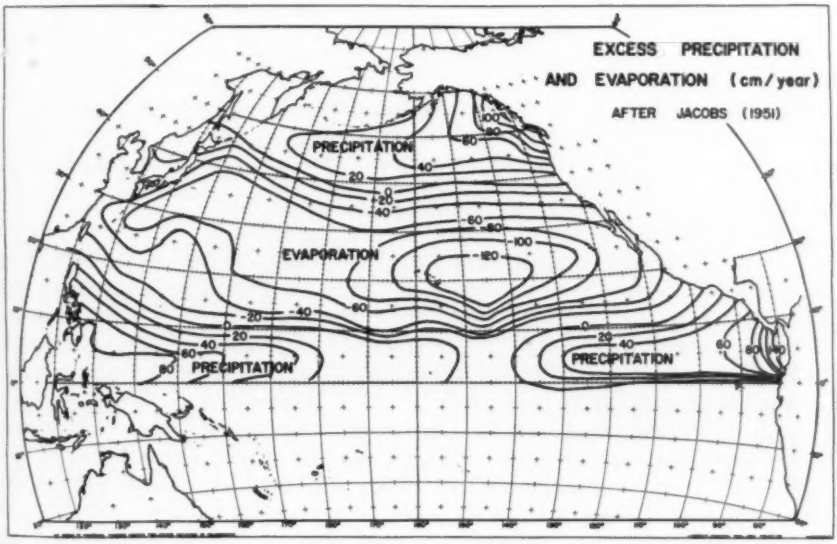


FIG. 7. Precipitation and evaporation.

creases with depth and vanishes when the rate of energy dissipation equals the rate of energy supply. Hence there is a lower limit of wind mixing which varies primarily with the wind force (Tabata and Giovando, 1962).

The resulting structures are irregular (Fig. 8). In a wind-mixing situation the depth of the surface layer is determined by the most recent strong winds. During periods of heating and light winds it contains small transient thermoclines which will vanish if cooling or strong winds occur (Tully and Giovando, 1963). Hence it is potentially but not always isothermal. The seasonal thermocline contains successive layers and gradients whose thickness varies from overlying microstructures to distinct separate thermoclines. The uppermost part of the thermocline is due to the most recent strong winds and heating. The deeper parts of the structure provide a historical record of the processes that created it.

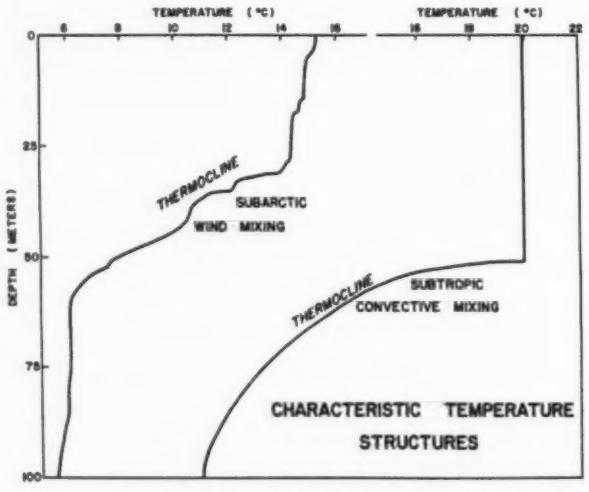


FIG. 8. Mixing structures.

Convective mixing occurs in any situation where the density of the surface waters is increased. Then they sink, mixing with the underlying waters to form a truly homogeneous layer to a depth limit determined by the density structure. This sinking erodes the top of the thermocline. At the limit of convection there is an abrupt boundary which may be regarded as a discontinuity in the structure, rather than a gradient.

Such convection may be either temperature or salinity driven. As waters cool their density increases and, in the absence of a salinity gradient, convection will occur. On the other hand, fresh water may be removed from the sea by evaporation or freezing so that the salt content and hence the density of the residual water increases. So it sinks.

Simple wind mixing creates an isothermal layer to a depth determined by the wind force and duration. Convection creates a mixed layer to a depth

determined by the density structure of the water. Convection will always increase the previous mixed layer depth. Hence when it occurs, convection determines the depth of the mixed layer, and wind mixing can be disregarded. The distinctive characters of the structures usually reveal which process is dominant.

In any season the depth of the potentially mixed layer (Fig. 9) indicates the balance between the local surface exchange and the downward mixing processes. The contours are not zonal.

This depth varies through an annual cycle whose range is approximately a function of latitude similar to the annual range of surface temperature (Fig. 6). The range is near zero in the tropics and increases northward to a maximum in the arctic. In the north it is shallowest at the end of the heating season and deepest at the end of the cooling season.

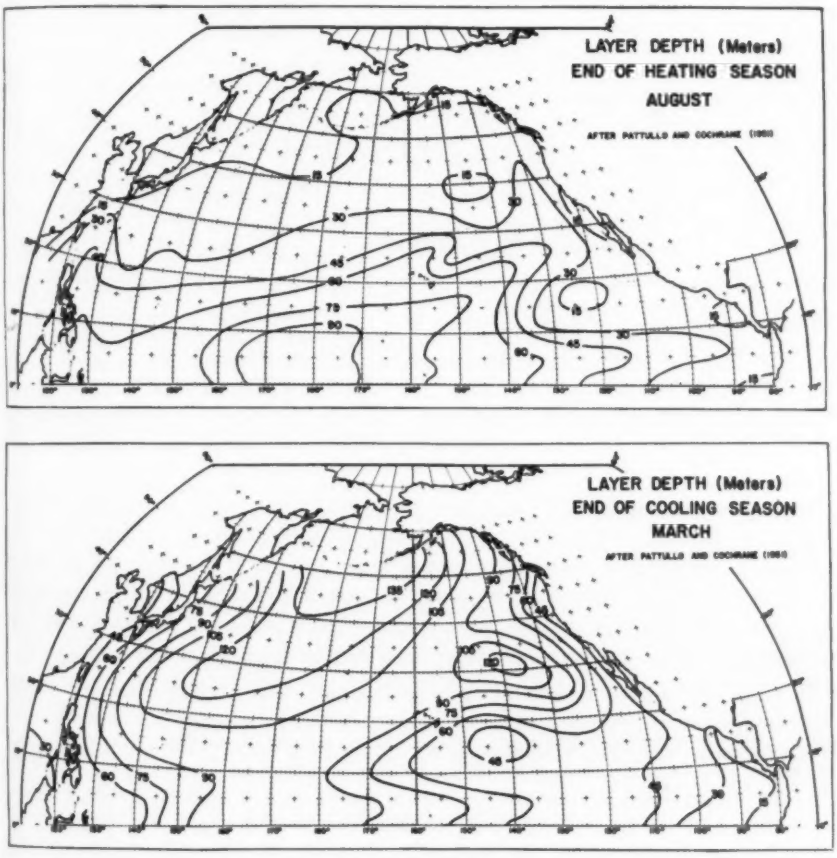


FIG. 9. Layer depth chart.

Internal Waves

In any natural fluid system there are internal oscillations in the continuum whose amplitude and frequency are inversely proportional to the density gradient. These oscillations can be recognized at any discontinuity, such as the sea surface or in the gradient of any property such as temperature.

Figure 10 shows the isotherms observed by Lee and LaFond (private communication) using a thermistor chain suspended from USS *Marysville* en route from Los Angeles to Honolulu during the summer of 1961. The undulations of the isotherms are attributed to internal waves. By comparison with Fig. 8 it is apparent that their amplitude and period are least in the most abrupt part of the thermocline and greatest at depths where the temperature gradient is least. After considerable investigation they concluded that the system included waves travelling in all directions and had a spectrum of period from a few minutes to at least half a day.

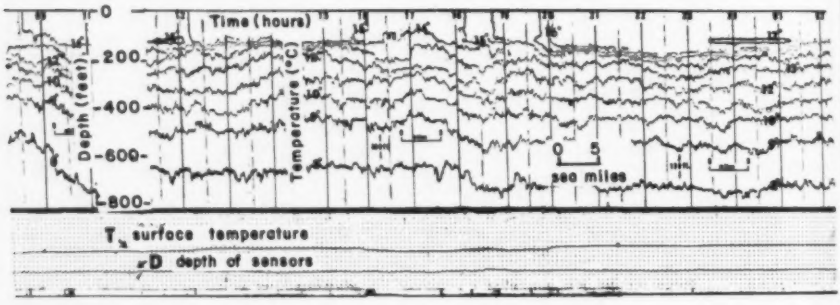


FIG. 10. Isotherms (1 C°) observed by Lee and Lafond (private communication) using a thermistor chain suspended from USS *Marysville* en route from Los Angeles to Honolulu during the summer of 1961.

Recent studies (Tabata and Giovando, 1962) of the data from Ocean Station "P" (Lat. 50°N, Long. 145°W) in the Subarctic Pacific showed that the standard deviation (two-thirds of the data) of the upper and lower limits of the seasonal thermocline from their mean positions was about ±4.5 m. Current research (Giovando, Robinson and Tripp, private communication) show that this standard deviation is about the same over the whole eastern North Pacific Ocean.

Also, it has been shown that the oscillations at the top and bottom of the thermocline have different periods and so are not always in phase. Consequently, the thickness of the thermocline may vary from 10 to 50 m (500%) in a few hours (Tully and Giovando, 1963).

It is evident that any assessment of the depth or dimensions of oceanographic structures such as the thermocline or halocline must be cognizant of the ambient variations due to internal waves.

REGIONS

Bringing all these considerations together in one diagram (Fig. 11) provides rational definitions of the oceanographic regions in the North Pacific Ocean. There are four regions of water mass formation where the transport is slow and/or zonal. In each of these the local surface processes are distinct. On the western boundary there are two regions where the water masses are transported more rapidly than they can adjust their properties. These come together in a Region of Confluence where the transported waters mingle. Finally, there is a system of coastal regions whose properties and structure are distinct from the oceanic regions.

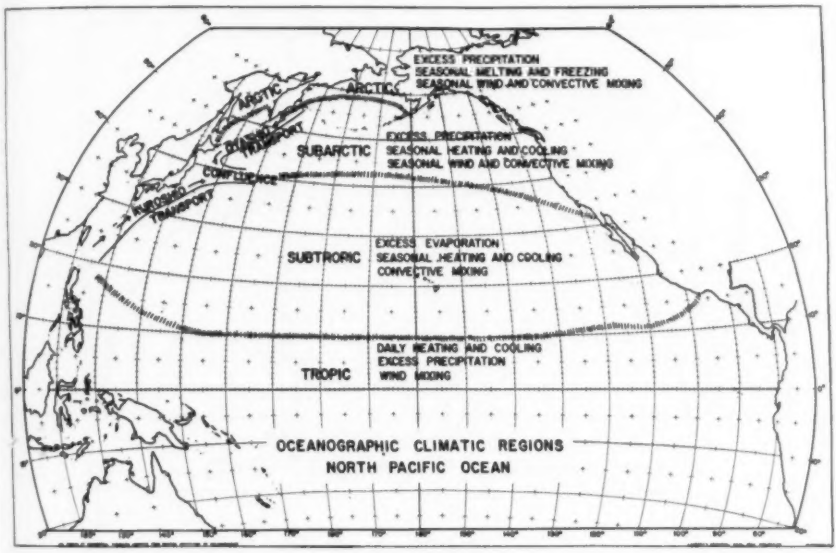


FIG. 11. Regions.

TROPICAL REGION (TROPICS)

The region of tropical structures lies between Latitudes 10°N. and 10°S. In the Pacific it extends half way around the world. In the eastern and western parts precipitation exceeds evaporation, but they are nearly equal in the middle (Fig. 7). This stabilizes the density structure so that wind is the dominant mixing factor. In general, daytime heating equals nighttime cooling throughout the year so that the temperature remains warm and constant. There are zonal flows with net westward transport so that the effects of the surface processes tend to accumulate to westward.

The temperature structure in the mid-ocean Tropics (upper diagram, Fig. 12) is characterized by a very deep potential layer containing a few transient structures. The temperature gradient in the main thermocline is approximately a function of the logarithm of depth (Tully, 1957) containing some irregularities in the upper part. Its bottom is not defined. In the salinity structure there are usually some small haloclines resulting in a salinity maximum near the

bottom of the potential layer. Below this, in the thermocline the salinity decreases slightly with depth.

The thermocline is much shallower towards the eastern limit where the zonal transport originates (Fig. 2) and is stabilized by excess precipitation. In mid ocean and the far west the great depth is due to the accumulation of waters in equilibrium with the atmosphere.

Since seasonal variations are small in the Tropics this structure persists throughout the year as indicated in the idea-gram model shown in the lower diagram (Fig. 12).

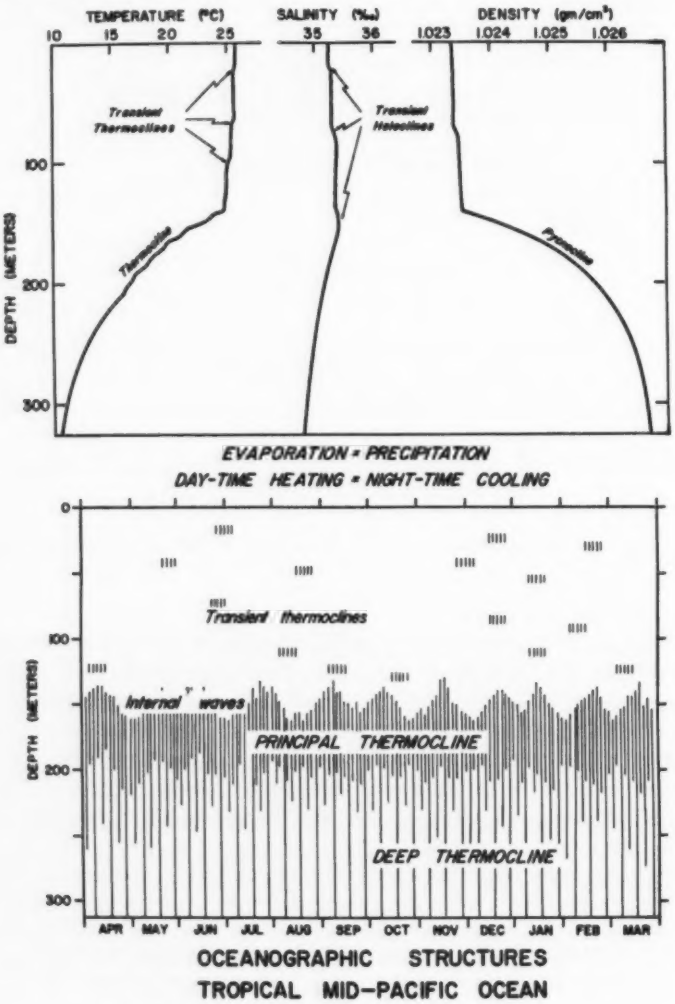


FIG. 12. Structures in the Tropics. Tropical model.

SUBTROPIC REGION (SUBTROPIC)

The Subtropic (Fig. 11) is the largest oceanographic region. It contains the great Subtropic Gyre (Fig. 2) in which the mid-ocean flows are zonal and the waters become adjusted to the surface processes. In the eastern part, the southward meridional flow is so slow that the seasonal waters tend to become adjusted to the surface processes en route. This region does not include the high-speed Kuroshio on the western boundary.

Evaporation exceeds precipitation throughout the year (Fig. 7). Fresh water is continually being removed from the surface leaving the salt in the sea.

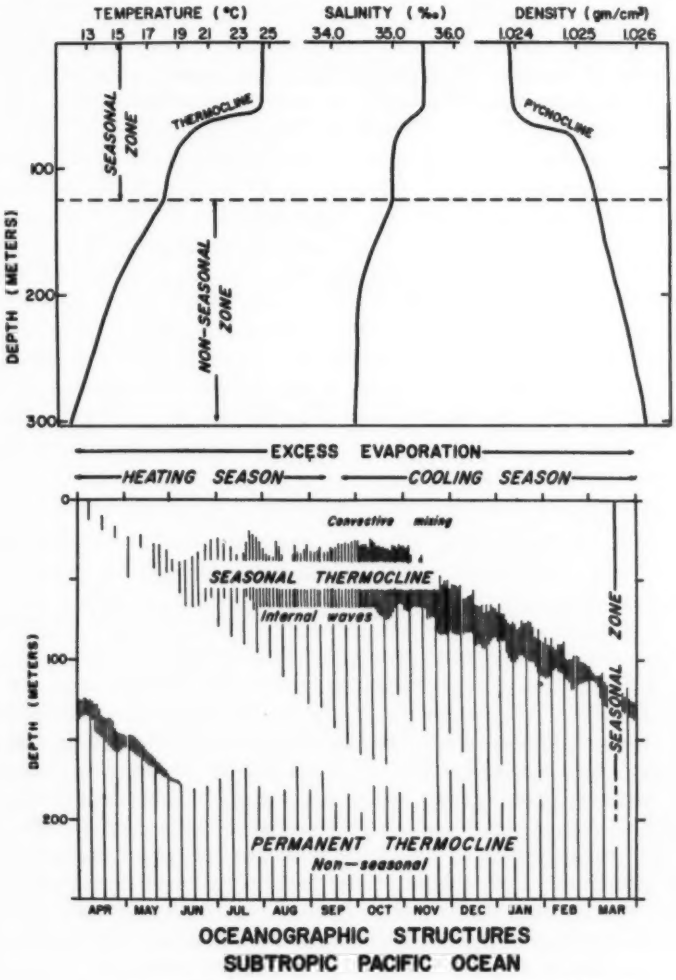


FIG. 13. Structures in the Subtropics. Subtropic model.

Despite the heating, evaporation-driven convection occurs frequently, particularly in mid ocean, and usually provides a truly mixed layer extending below the depth of simple wind mixing (Fig. 13). This process is identified by the abrupt character of the top of the thermocline. The temperature structure in the thermocline is approximately a function of the logarithm of depth. In the thermocline, the salinity decreases to a minimum between 200 and 800 m depth. Throughout this region the density structure is primarily a function of the temperature structure.

In the Subtropic Region there is a seasonal cycle of heating and cooling similar to that shown in Fig. 4. From the spring to autumn equinox, daytime heating generally exceeds nighttime cooling. Heat accumulates in the sea so that the surface waters are warmest in September. Cooling is dominant during the remainder of the year so that the waters are coldest at the end of March. The annual range of temperature (Fig. 6) increases northward from zero in the Tropics to a maximum of 8 C° between 40° and 45°N. latitude.

The sequence of growth and decay of the seasonal thermocline is illustrated in the lower diagram of Fig. 13. At the end of the cooling season the waters are isothermal to about 150 m depth. Soon afterwards, at the beginning of the heating a season thermocline is formed between 40 and 60 m depth, separating the warmed and unwarmed waters. As the upper waters are warmed, the temperature difference through the thermocline (magnitude) grows, while its depth (position) remains nearly constant. During the cooling season the upper waters cool and the convection process is accelerated. In consequence the thermocline is eroded and sinks to the limit of the seasonal zone (about 150 m). In the Subtropic Region these seasonal waters never become as cold as the deep non-seasonal waters. Hence, there is a deep permanent thermocline in the non-seasonal zone below 150 m depth.

Subarctic Region (Subarctic)

The Subarctic Region (Fig. 11) contains several gyres which taken together provide cyclonic circulation around the region and through the Arctic. It has been described in detail by Uda (1963) and Dodimead *et al.* (1963).

The Subarctic is distinguished by excess precipitation (Fig. 7) which creates a distinctive salinity structure (Fig. 14). The accumulated fresh water is contained in an upper, near isohaline zone, from the surface to about 100 m depth. Below this, between about 100 and 200 m depth, there is a permanent halocline, in which the salinity increases about 1‰ to 33.8‰. This zone marks the ultimate limit of local surface seasonal effect. Below this, the salinity increases into the abyss. There is no salinity minimum in the Subarctic or Arctic Pacific, and the density is primarily a function of the salinity structure.

The seasonal behaviour of the thermocline has been described by Tully and Giovando (1963) and is illustrated in the lower diagram of the figure. At the end of the cooling season the waters are homogeneous to the permanent halocline (about 100 m depth). In April, a thermocline forms in the near isohaline upper zone, between 25 and 50 m depth, and its magnitude increases as the surface waters are warmed. Because of the excess precipitation there is a small halocline

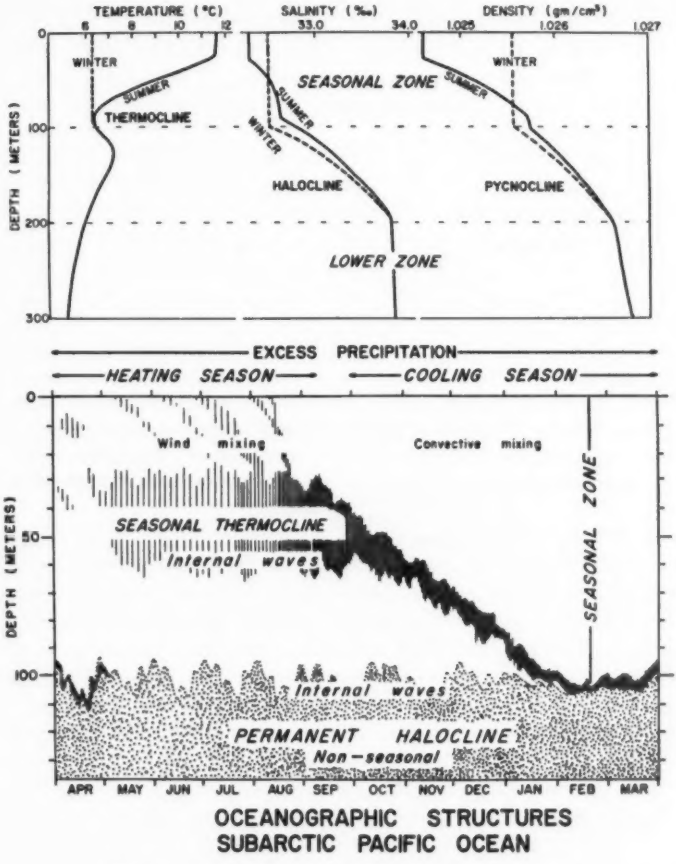


FIG. 14. Structures in the Subarctic. Subarctic model.

associated with this seasonal thermocline. Convection cannot occur. Mixing is due to wind alone. The potential layer contains transient thermoclines whenever the weather is fine.

During the cooling season, from September, the waters cool and temperature-driven convection occurs despite the excess precipitation. The thermocline is eroded and sinks. The residue reaches the top of the permanent halocline (100 m) during January or February. Thereafter these waters remain homogeneous and continue to cool until the end of the cooling season in late March. In the northern parts of the region they frequently become colder than the water in the permanent halocline.

Between the seasonal thermocline and the halocline there is a sub-thermocline layer in which the isothermal temperature structure created during the previous winter is preserved.

PACIFIC ARCTIC REGION (ARCTIC)

The Arctic Regions in the Pacific (Fig. 11) are in the northern Bering and Okhotsk Seas where ice forms during the winter. These areas are really subregions of the Subarctic. They are subject to excess precipitation and there is a halocline in the salinity structure.

The Pacific arctic behaviour model is shown in Fig. 15. As elsewhere, warming commences in April soon after the spring equinox. From then until the summer solstice the heat is expended in melting the ice. Because sea ice contains very little salt this process releases fresh water which forms a shallow brackish layer. Warming does not commence until most of the ice has vanished in mid summer. Thereafter, during the long northern days, warming is rapid and the shallow, halocline-bound surface layer warms to more than 7°C. The seasonal halocline is the dominant feature of structure and controls the depth of the thermocline.

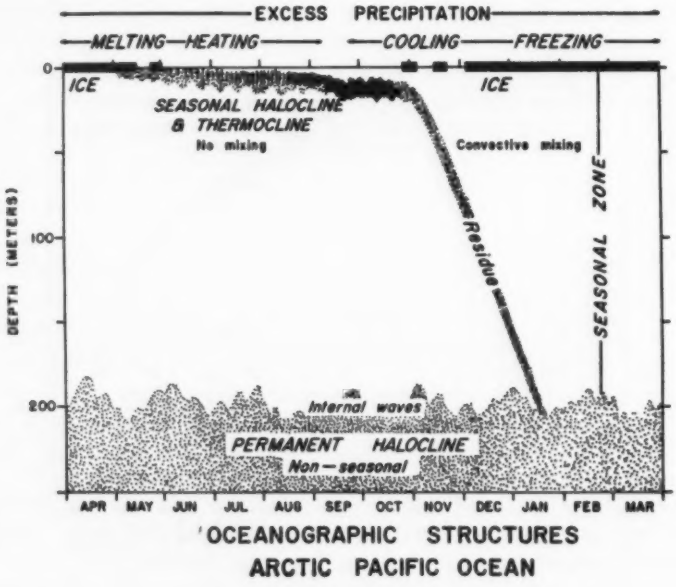


FIG. 15. Arctic model.

During the first few months of the cooling season, the heat is lost, and the thermocline vanishes. It cannot sink because it is stabilized in the shallow brackish layer of ice-melt water. As winter advances freezing occurs. The formation of ice removes fresh water from the sea, leaving the salt in the residual water. Its salinity increases; it becomes more dense than the underlying water and convective mixing occurs. Hence the residue of the halocline sinks. These residues from successive annual cycles accumulate in the deep permanent halocline, which in these seas extends from 100 to 500 m depth. In the zone between

the ice and the permanent halocline the waters are homogeneous at freezing temperature, and colder than the underlying waters.

Transport Regions

Wherever western boundaries occur in the ocean the meridional flows of the gyre systems are intensified and become streams (Munk and Carrier, 1950) (Fig. 2) whose rate of flow is of the order of 25–70 miles/day. They transport waters between regions of zonal flow, where the regional properties and structure of the waters are acquired. At least one heating or cooling season is required to establish these regional properties. It is evident that while the western boundary streams remain coherent, they transport the structure and properties of the water from one part of a region to another, more rapidly than the waters can adjust to the changing climatic processes. Hence, such streams can always be distinguished from the neighbouring waters by their transported characteristics.

In these regions the effects of the normal regional processes are superimposed on the transported features, which may or may not be erased depending on their depth.

Kuroshio

Kuroshio (Fig. 16) is the western boundary stream of the Subtropic Gyre. It flows from the southern to the northern part of the Gyre. It carries the thick layer of saline, warm water generated in and near the Tropics from the vicinity of the Philippine Islands past the coast of Japan. It loses heat en route but never becomes fully adjusted to the changing surface climate. It is estimated that 50% of the heat in the waters off Japan is carried into the area by Kuroshio (Masuzawa, 1952).

There is considerable coherence in the stream, so that its boundaries may be readily recognized by marked horizontal gradients of temperature and layer depth which are analogous to weather fronts. These features become more marked to northward along the line of flow and are the outstanding characteristics of the stream off the Japanese Islands.

Analogous to the Gulf Stream in the Atlantic, the stream meanders, and the meanders progress along the stream so that the detail of structure is dynamic and ever-changing. Some authors (von Arx, 1962) describe such streams as a sequence of large eddies drifting along the line of transport. Presumably each eddy is distinct and may move rapidly at one time and slowly at another, and has considerable internal circulation.

Local surface processes act on these waters. There is a normal annual sequence of growth and decay of the seasonal thermocline. However, this is shallower than the thick transported structure and does not erase it. Usually the seasonal sequence is ignored in the presence of the more spectacular mobile frontal structures.

Because the stream is coherent there is a marked correlation between the gradient of surface temperature and the layer depth. The layer depth is deepest in the warmest water. This correlation may be obscured in a locality or eddy where a strong seasonal thermocline develops.

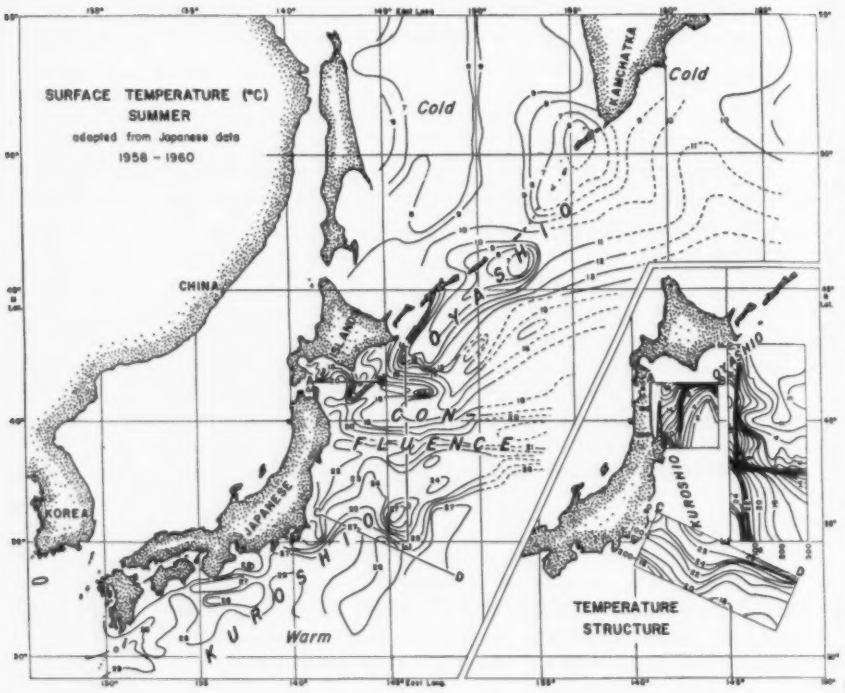


FIG. 16. Western boundary regions.

OYASHIO

The western boundary stream of the Subarctic Gyre originates in the Western Bering Sea. It flows south along the Kamchatka Peninsula, into and around the Okhotsk Sea. It becomes the Oyashio when it flows into the Pacific through the Kurile Islands past northern Japan. The rate and volume of this transport are very much less than in the Kuroshio. The coast-hugging flow amounts to peripheral transfer through three sub-gyres (Dodimead *et al.*, 1963) in the Arctic Region. In these areas there are no marked boundaries. Rather the structure grades from Arctic to Subarctic over considerable distances.

The flow is strongest in summer when it is accelerated by the ice-melt water. Then, there are shallow coincident thermoclines and haloclines (Fig. 15). During the winter the flow slackens and the waters cool to freezing.

CONFLUENCE REGION

Kuroshio and Oyashio meet in a Region of Confluence (Fig. 16) off northern Japan and turn eastward, side by side. Here the frontal distinction between the water masses becomes extreme (see inset, Fig. 16). In general the sea surface temperature changes about 15 C° in less than 200 miles. Within this distance there are fronts as great as 5 C° in a mile or so, resulting from the peri-

pheral turbulence. Eddies of water break off from one stream and are occluded in the other. These eddies drift eastward, rotating and mixing with the surrounding waters and eventually lose their identity.

From the Region of Confluence, the waters are dissipated eastward in the slow eastward trans-ocean flow (Fig. 2). At the origin, the flow may be regarded as extensions of the parent streams. In fact they are frequently called the Kuroshio and Oyashio extensions. However, recalling the marked seasonal cycles and ranges of the surface processes in these latitudes, it is evident that the original features must be erased in one heating and cooling season. It requires more than 2 years for the West Wind Drift to cross the ocean from Asia to America (Uda, 1963). In this time the zonal surface processes fully re-establish the regional properties and structures of the waters.

Domains

This discussion has considered only the major climatological regions in the ocean. It is obvious to any student of oceanography that these regions can be subdivided into domains based on additional considerations of oceanographic and meteorological mechanisms. Through the researches of Dodimead *et al.* (1963) this has been accomplished in the Subarctic and Arctic Pacific as shown in Fig. 17. This concept can be extended to the other regions of the North Pacific by similar studies of existing data.

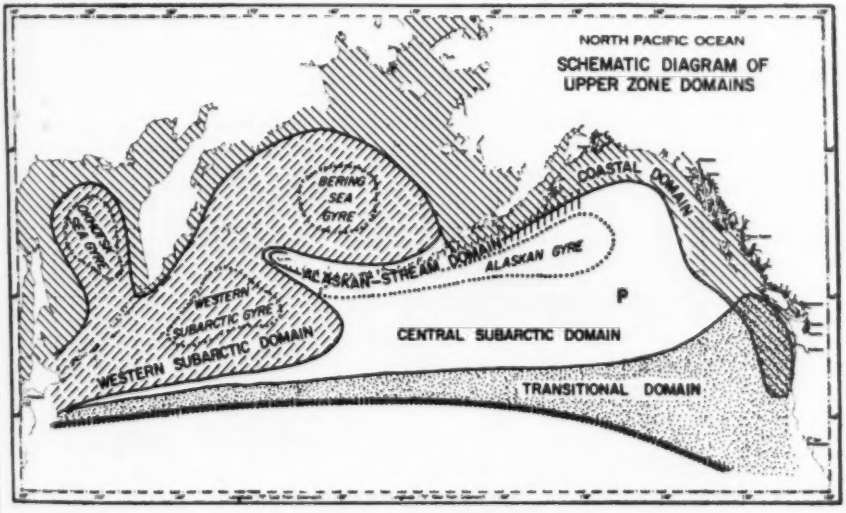


FIG. 17. Upper zone domains.

Coastal Region

All coastal waters over the continental shelves are subject to the same surface processes as the oceanic waters. However, these are usually modified by the proximity of shore and bottom. Also, the coastal waters are subject to

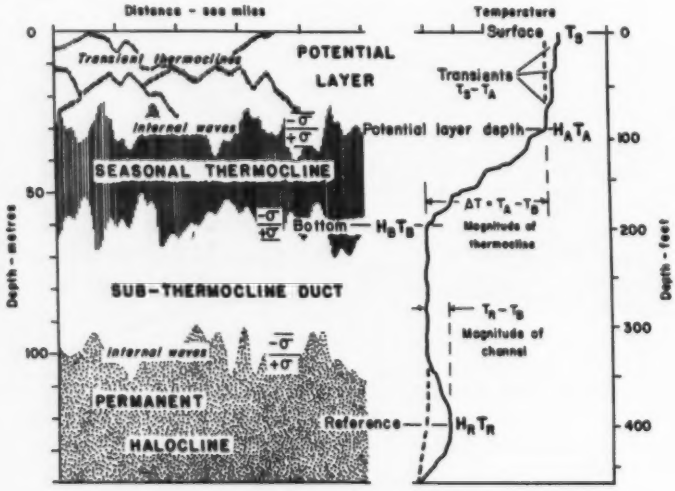
dilution by land drainage, transport by coastal currents, and mixing and local gyre formation by tidal currents. The Coastal Region is a sequence of micro-domains, each with its own oceanographic characters. Some of these have been studied and some generalizations have been made in all parts of the world.

CHARTING TEMPERATURE STRUCTURE

These considerations define the parameters required to assess the temperature structure in the seasonal zone. To facilitate the discussion it is convenient to transpose the standard presentation of structure as shown on the right of Fig. 18 to the idea-gram shown on the left. There is a potentially isothermal layer which may or may not contain transients. There is a seasonal thermocline, in which the gradients may be regular or irregular. Below this is a sub-thermocline layer in which the gradients are less than in the thermocline. Where there is a halocline (Subarctic and Arctic) it limits the depth of surface seasonal processes. Usually it contains a temperature increase which is a non-seasonal feature. If there is no halocline (Subtropic and Tropics) there cannot be a temperature increase in the deep water below the seasonal zone.

Superimposed on these features, there are various kinds of short-term fluctuations which have varying degrees of significance. Appreciation of these ever-changing conditions requires frequent, repetitive observation and collation, similar to the Weather Service procedures.

Two approaches are required. In the slow-moving, non-turbulent regions, it is within the foreseeable state of the oceanographic art to assess and forecast the structure from adequate knowledge of heat budget, surface winds, and historical data. This requires a modest extension of the type of research that



OCEAN analysis of structure
Subarctic Pacific Ocean

FIG. 18. OCEAN interpretation of structure.

has been done to define oceanographic structure and behaviour at Ocean Station "P" (Tabata, 1961; Tully and Giovando, 1963) and means, such as satellite observations and analyses by numerical weather facilities, to compute the daily heat budget over the ocean in some detail (USBCF, 1964). Meanwhile, assessments may be made on the basis of the regional models shown here, aided by accumulated experience (Giovando, MS, 1962) and bathythermograph and surface temperature observations. Usable, but not ideal forecasts are made by intuitive or hand calculated appreciation of the existing heating-cooling conditions and wind (Fig. 19) (Tabata and Giovando, 1962).

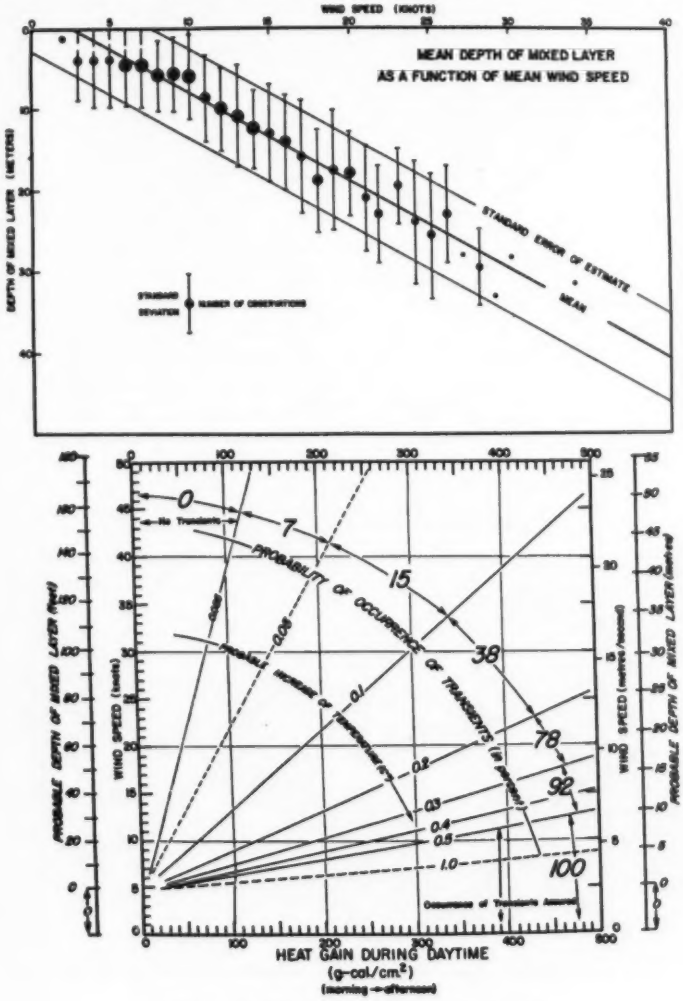


FIG. 19. Occurrence of transients (Tabata).

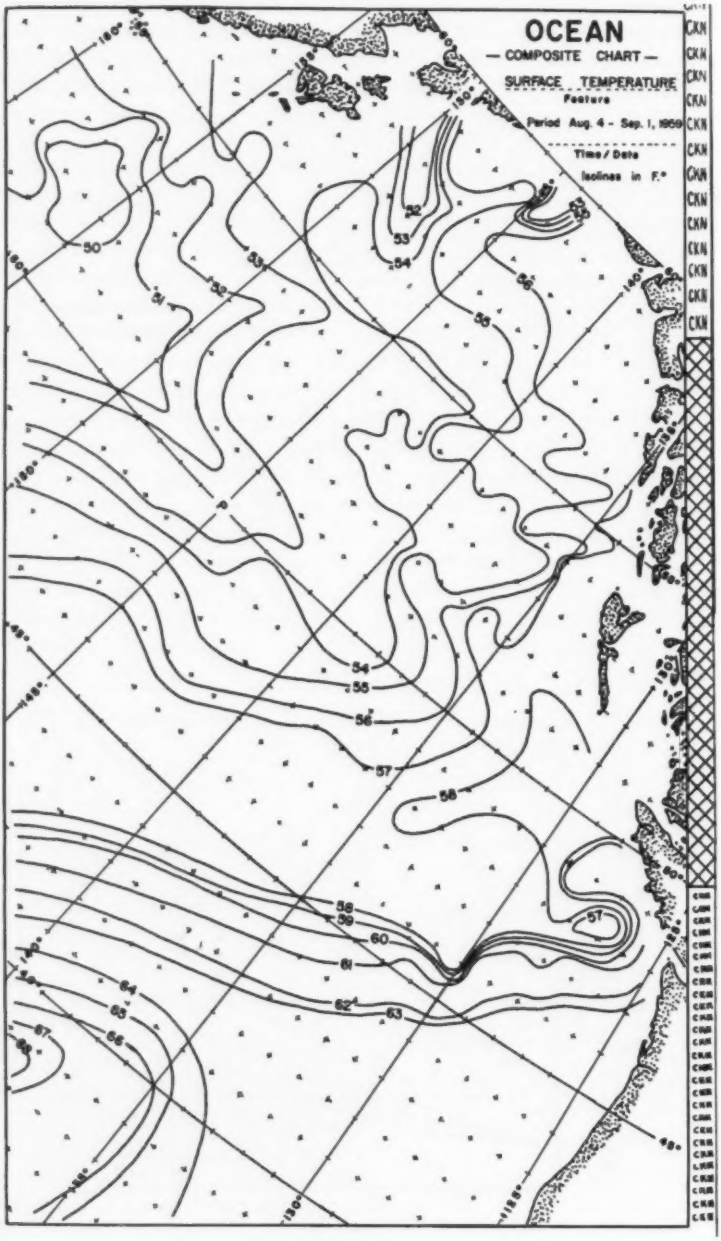


FIG. 20. OCEAN Chart — surface temperature.

In the Transport and Confluence Regions (western boundary regions) the effects of local surface weather are secondary to the effects of transport and turbulence. Knowledgeable observation requires networks of continuous surface temperature recordings to define the location and extent of water masses and their boundaries, and bathythermograph observations to define the structure within the water masses. The surveys should be repeated at frequent intervals so that, by comparison of successive charts, the movement and behaviour of the features can be recognized and extrapolated.

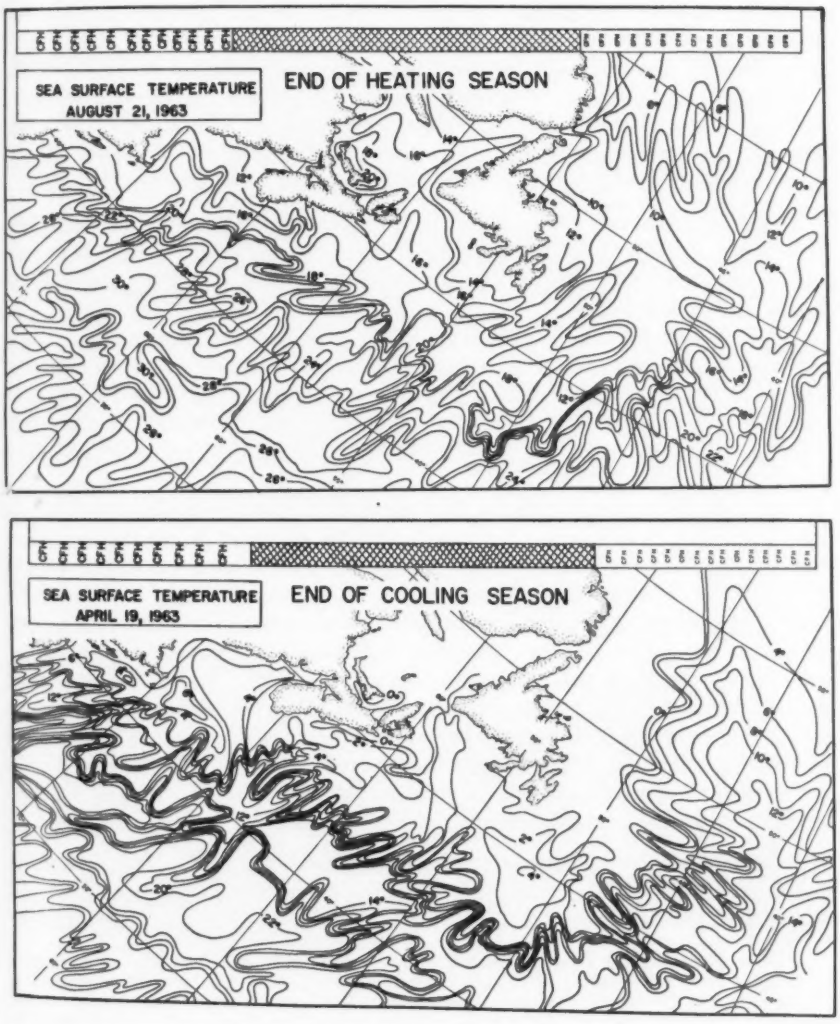


FIG. 21. East coast — surface temperature.

The temperature structure can be adequately defined by the depth and temperature limits of the zones. The small variations within the zones are transient. Their occurrences and total magnitude must be recognized, but their individual positions and magnitudes cannot be stipulated.

The desired features are defined in Fig. 18 and may be charted.

SURFACE TEMPERATURE (FIG. 20)[4]. For most purposes it is only necessary to know the surface temperature to the nearest Celsius degree. In the slow-moving oceanic regions, weekly or monthly temperature charts are adequate to define the seasonal and annual changes (USBCF, 1960). However, well-defined surface temperature charts reveal the occurrence and location of fronts (Fig. 21). Ideally, fronts should be identified from continuous recordings. In the Transport and Confluence Regions, where the fronts are conspicuous and considerable data are available from transitting ships via the Weather Services, respectable interpretations can be made. Comparison of successive charts permits assessment of the behaviour of the fronts and, possible extrapolation.

POTENTIAL LAYER DEPTH (FIG. 22). This should include the average depth to the top of the seasonal thermocline, with standard deviation due to internal waves and other variability. It should show, by shading, areas where significant transient thermoclines occur.

At present, the layer depth is determined from bathythermograms. It is desirable to make sufficient sequential observations to define the mean value and standard deviations (OCEAN procedure) (Giovando, MS, 1962). Recent research indicates that in the central and eastern ocean regions the standard deviation is about ± 4.5 m. Where observations are limited, this variability should be assumed.

The regional models indicate that sophisticated methods can be used. In the Kuroshio and Confluence Regions the layer depth may be related to surface temperature. In the Tropics it may be evaluated from historical data. In the Subtropics it depends on wind mixing and, to a greater extent, on convection due to evaporation during the heating season, and on convection due to evaporation plus cooling in winter. Research is required to define these relations. Meanwhile, historical charts provide an acceptable guide. In the Subarctic and Arctic, during the heating season, layer depth is a function of wind-force history (Fig. 19) (Tabata and Giovando, MS, 1962). During the cooling season it is a convection function, which has not been solved.

Daily charts are required in the transport regions. In other oceanic regions, weekly, and in some seasons, monthly charts are adequate for most purposes.

DEPTH OF THE BOTTOM OF THE THERMOCLINE (FIG. 23). This feature is distinct (minimum temperature) in parts of the Arctic, Oyashio, Confluence, and Subarctic Regions. It is not distinct in the Tropic, Subtropic, Kuroshio, or

[4]Figures 20 through 25 are reproductions of charts prepared by the Canadian Oceanographic Information Service (Giovando, 1961) in the Royal Canadian Naval Weather Service at Halifax, Nova Scotia (Fig. 21) and at Esquimalt, British Columbia. The charts are prepared on the conic projection compatible with weather maps. The size and format (border, etc.) are designed to suit the radiofacsimile broadcast equipment.

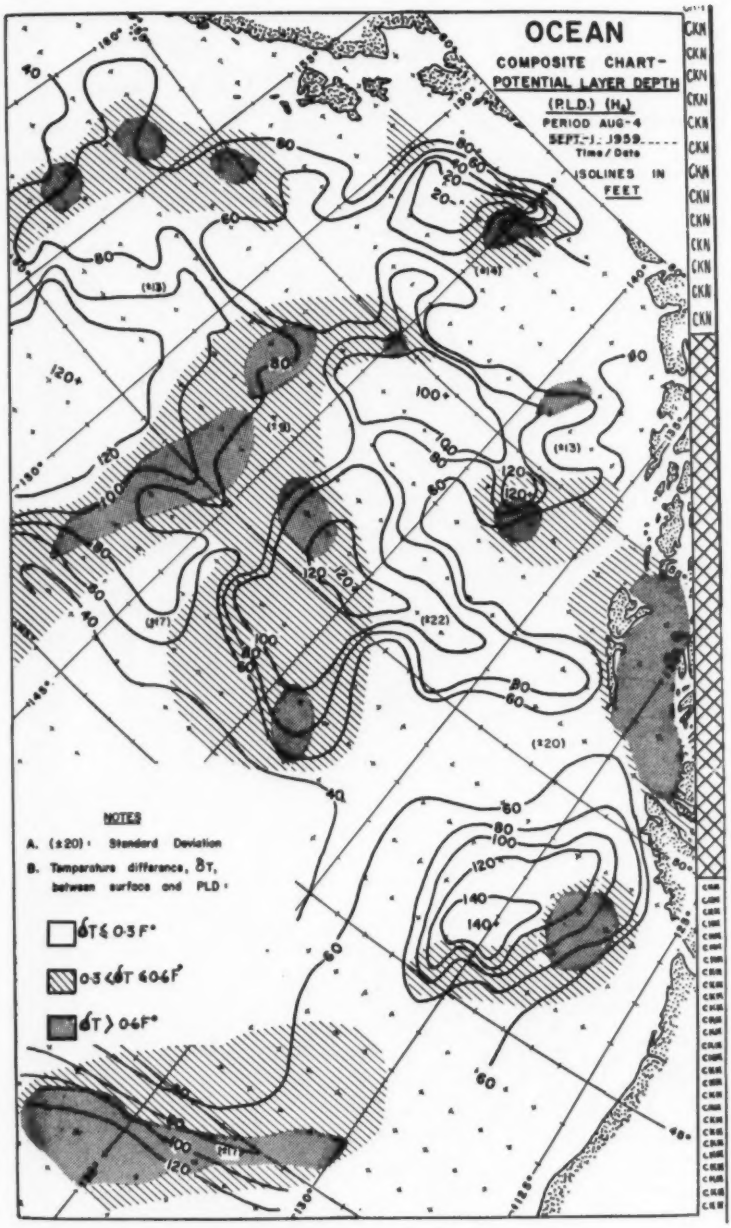


FIG. 22. OCEAN Chart — potential layer depth.

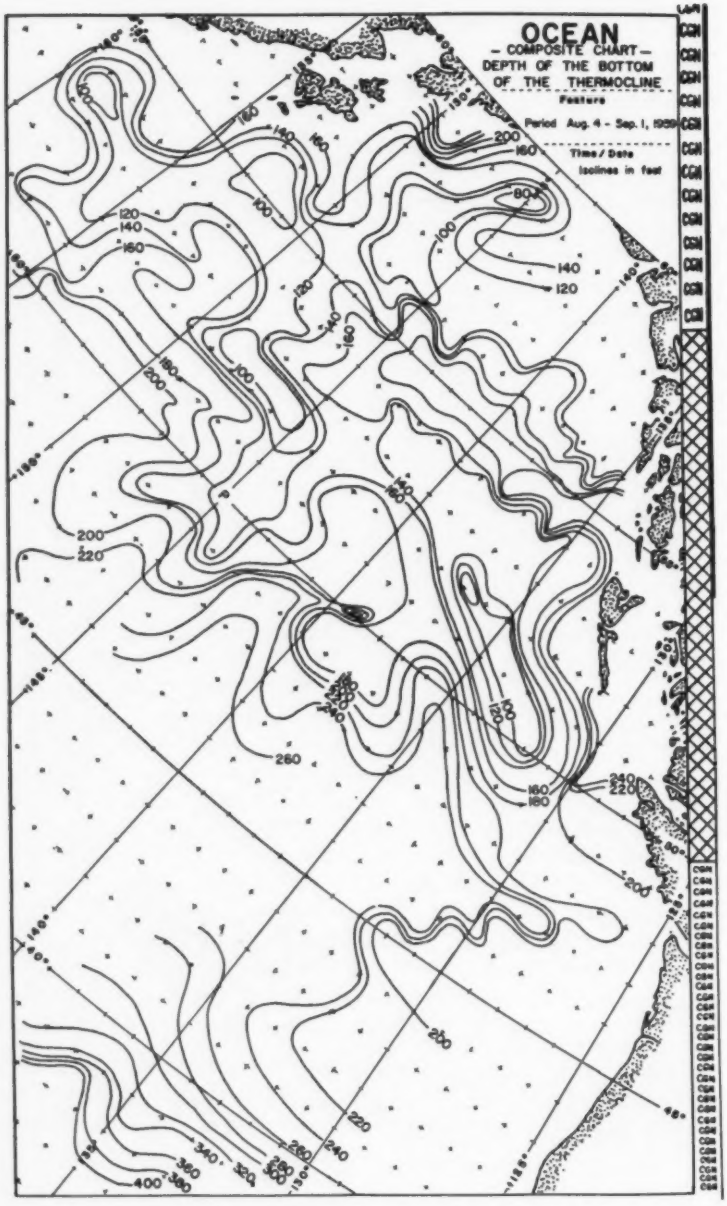


FIG. 23. OCEAN Chart — bottom of the thermocline.

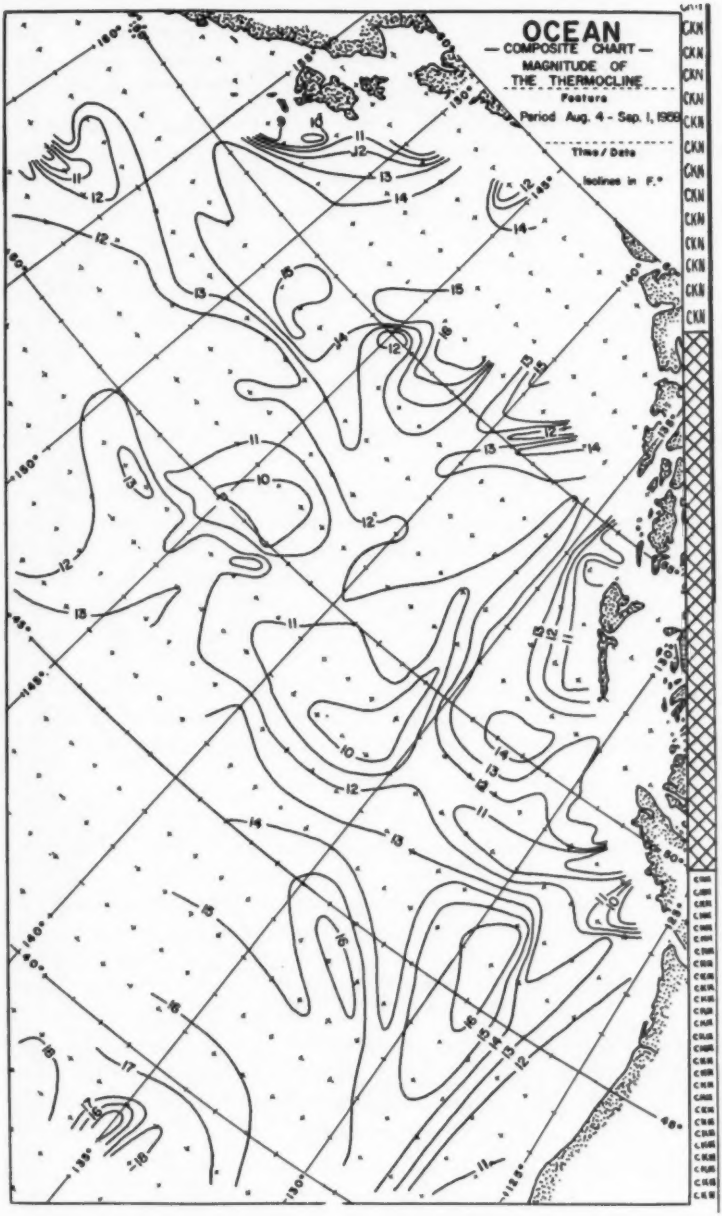


FIG. 24. OCEAN Chart — magnitude (ΔT) of thermocline.

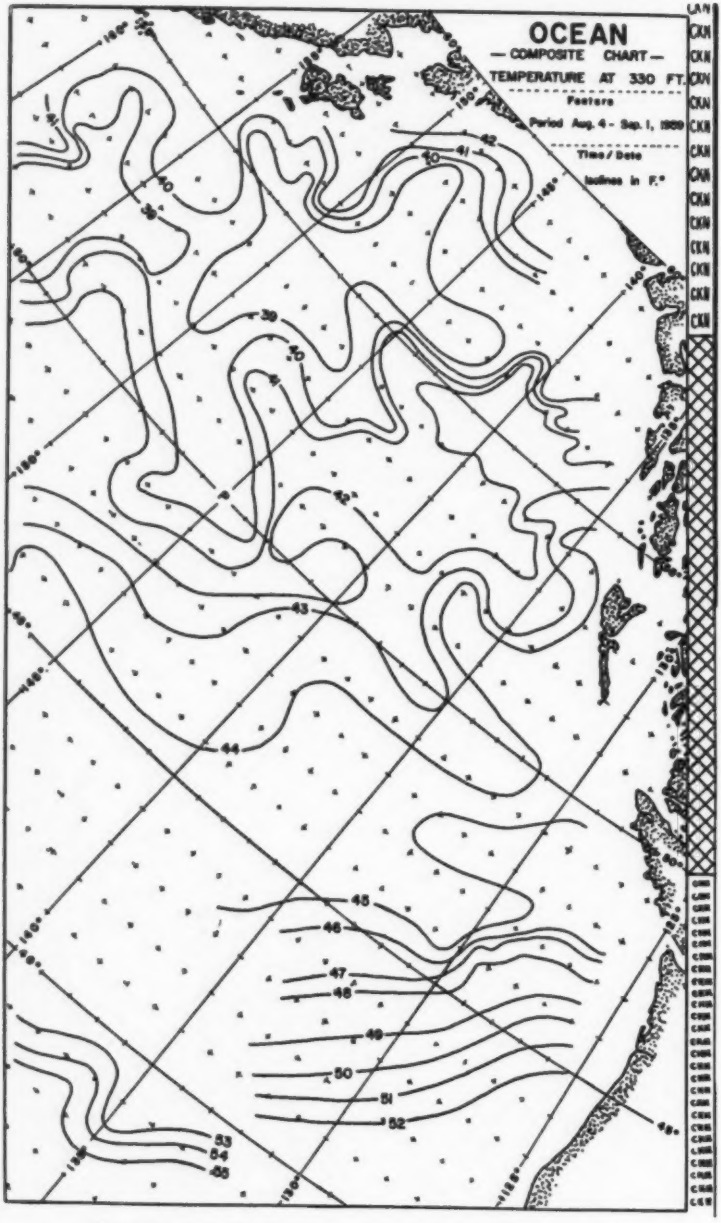


FIG. 25. OCEAN Chart — temperature at the reference depth.

Transitional Regions. The character of the sub-thermocline structure (negative, isothermal, or positive) may be shown by shading.

TEMPERATURE MAGNITUDE OF THE THERMOCLINE (FIG. 24). This value defines the significance of the thermocline as a boundary to fish movements, etc. Daily to weekly charts are required in the Transport Regions. In other seasonal regions weekly charts are required during spring and autumn when the values are small and changing rapidly. A historical chart is adequate in the Tropics.

REFERENCE DEPTH. The reference depth is the ultimate limit of surface induced seasonal effects (e.g. winter cooling). At and below this limit the properties and structure vary with location but are practically constant with time and may be assessed from historical data in permanent charts. However, it must be realized that the reference depth has a different significance in each oceanographic region. In the Tropic Region it may be taken as the layer depth (about 150 m). In the Subtropic Region it is the depth at which the seasonal cycle of temperature vanishes (about 130 m). In the Subarctic Region it is the top of the permanent halocline (about 110 m). In the Transport Regions this depth varies with location.

TEMPERATURE AT THE REFERENCE DEPTH (FIG. 25). This value varies with position but is nearly constant with time, while the seasonal thermocline exists from April through November. It may be charted by accumulating data from bathythermograms during a season. Alternatively, historical charts may be used with considerable confidence.

The magnitude (ΔT, etc.) of the surface-induced effects in the overlying seasonal zone may be measured by comparing frequent observations of the surface temperature with historical charts of the temperature at the reference depth. This allows the use of shallow, high-speed sensing devices such as recording thermometers in ships and airborne radiation thermometers (Tully, MS, 1961).

CONCLUSIONS

From these discussions it is evident that the assessment of temperature structure and behaviour must be based on the models which vary from one oceanic region (or domain) to another. However, despite these very great regional differences the significant features of temperature structure can be shown in a limited number of charts whose data content and format are universally consistent.

Obviously the concepts presented here, for the North Pacific Ocean, can be extended to other oceans and seas.

No part of this discussion is new. Rather it is an attempt to collate existing information into a complete philosophy which may be applied consistently in all ocean areas, and be intelligible to all users.

REFERENCES

DODIMEAD, A. J. 1961. Some features of the upper zone of the Sub-arctic Pacific Ocean. *Intern. North Pacific Fish. Comm., Bull.* No. 3, pp. 11–24.

DODIMEAD, A. J., F. FAVORITE AND T. HIRANO. 1963. Review of oceanography in the Subarctic Pacific Region. *Intern. North Pacific Fish. Comm., Bull.* No. 13, 195 pp.

DOE, L. A. E. 1955. Offshore waters of the Canadian Pacific coast. *J. Fish. Res. Bd. Canada*, **12**(1): 1–34.

GIOVANDO, L. F. MS, 1961. The Canadian oceanographic information service. *Fish. Res. Bd. Canada, Pacific Oceanogr. Group Circular* 1961–18, 17 pp.

MS, 1962. The OCEAN system of assessment of bathythermograms. *Fish. Res. Bd. Canada, MS Rept. (Oceanogr. and Limnol.)*, No. 105, 62 pp.

JACOBS, W. C. 1951. The energy exchange between sea and atmosphere and some of its consequences. *Bull. Scripps Inst. Oceanogr.*, **6**(2): 27–122.

JAPANESE DATA. 1958–1960. The results of meteorological and oceanographical observations. Japan Meteorological Agency, Tokyo; No. 23, January–June, 1958 (240 pp); No. 28, July–December, 1960 (304 pp).

MASUZAWA, J. 1952. On the heat exchange between sea and atmosphere in the southern sea of Japan. *The Oceanographic Magazine, Cent. Obs. Japan, Tokyo*, **4**(2): 49–55.

MUNK, W. H., AND G. F. CARRIER. 1950. The wind driven circulation in ocean basins of various shapes. *Tellus* Vol. 2, pp. 158–167.

PATTULLO, J. G., AND J. D. COCHRANE. MS, 1951. Monthly thermal condition charts for the North Pacific Ocean. *Scripps Inst. Oceanogr. Bathythermograph Section, MS Rept. No. 3.*, 30 pp.

REID, J. L. 1961. On the geostrophic flow at the surface of the Pacific Ocean with respect to the 1000 decibar surface. *Tellus*, **13**(4): 490–502.

TABATA, S. 1961. Temporal changes of salinity, temperature and dissolved oxygen content of the water at Ocean Station "P" in the northeast Pacific Ocean and some of their determining factors. *J. Fish. Res. Bd. Canada*, **14**(3): 241–319.

TABATA, S., AND L. F. GIOVANDO. MS, 1962. Prediction of transient temperature structures in the surface layers of the ocean. *Fish. Res. Bd. Canada, MS Rept. (Oceanogr. and Limnol.)*, No. 132, 17 pp.

TULLY, J. P. 1949. Oceanography and prediction of pulp mill pollution in Alberni Inlet. *Bull. Fish. Res. Bd. Canada*, No. 83, 169 pp.

1957. Some characteristics of sea water structure. *Proc. 8th Pacific Science Congress* (1953), Vol. 3, pp. 643–661. Philippines.

MS, 1961. Assessment of temperature structure in the eastern subarctic Pacific Ocean. *Fish. Res. Bd. Canada, MS Rept. (Oceanogr. and Limnol.)*, No. 103, 40 pp.

TULLY, J. P., AND F. G. BARBER. 1960. An estuarine analogy in the subarctic Pacific Ocean. *J. Fish. Res. Bd. Canada*, **17**(1): 91–112.

TULLY, J. P., AND A. J. DODIMEAD. 1957. Properties of the water in the Strait of Georgia, British Columbia and influencing factors. *J. Fish. Res. Bd. Canada*, **14**(3): 241–319.

TULLY, J. P., AND L. F. GIOVANDO. 1963. Seasonal temperature structure in the eastern Subarctic Pacific Ocean, pp. 10–36. *In* M. J. Dunbar, (ed.) Marine Distributions. The Royal Society of Canada, Spec. Publ. No. 5, Univ. Toronto Press.

UDA, M. 1963. Oceanography of the Subarctic Pacific Ocean. *J. Fish. Res. Bd. Canada*, **20**(1): 120–179.

U.S.B.C.F. 1960. (U.S. Bureau of Commercial Fisheries) Biological Laboratory, San Diego, Sea surface temperature charts, Eastern North Pacific Ocean. Published monthly in California Fishery Market News Monthly Summary, Part II – Fishing Information, San Diego.

1962. (U.S. Bureau of Commercial Fisheries) Biological Laboratory, Stanford. Monthly mean charts, sea-surface temperature, North Pacific Ocean. U.S. Bur. Comm. Fish., Circular 134, Washington. 36 pp.

1964. (U.S. Bureau of Commercial Fisheries) Biological Laboratory, San Diego. Information circular for marine weather observation summary for the Pacific Ocean.

VON ARX, W. S. 1962. An introduction to physical oceanography. Addison-Wesley Pub. Co. Inc. Reading, Mass. 422 pp.

Redescription of the Parasitic Isopod *Holophryxus alaskensis* Richardson, and a Note on Its Synonymy[1]

By T. H. Butler

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Full descriptions of both sexes of *Holophryxus alaskensis* Richardson are given. The host is the decapod *Pasiphaea pacifica* Rathbun. *Holophryxus californiensis* Richardson and *Hypodajus georgiensis* Nierstrasz and Brender à Brandis are considered synonymous with *Holophryxus alaskensis*. The generic name *Hypodajus* Nierstrasz and Brender à Brandis is a synonym of *Holophryxus* Richardson. The type-species of *Holophryxus* remains as *H. alaskensis*.

INTRODUCTION

The genus *Holophryxus* (Family Dajidae) was established by Richardson (1905a) with the type-species *H. alaskensis*. The diagnosis was based on three females collected in 1903 by the United States Bureau of Fisheries steamer *Albatross* in Behm Canal and Lynn Canal, Alaska, at 147–350 fathoms. No male was collected and the host was unknown. Later, Richardson (1908) described a second species, *H. californiensis*, on the basis of two specimens, one collected in Santa Barbara Channel, California, at 280 fathoms, and the other in Behm Canal, Alaska, at 150–280 fathoms. A male accompanied the female found in Santa Barbara Channel, and the female from Behm Canal was attached to the shrimp *Pasiphaea pacifica*. The male of *H. californiensis* was described in some detail, but the description of the female was inadequate.

On the basis of one female specimen with accompanying male, found on a pasiphaeid shrimp from the Strait of Georgia, British Columbia, Nierstrasz and Brender à Brandis (1931) set up the genus *Hypodajus*, with the type-species *H. georgiensis*.

During the course of exploratory fishing conducted by this Board's Biological Station at Nanaimo in 1953 and 1954, 18 female specimens of *Holophryxus* were taken in small-meshed trawls. All specimens were caught at 8 localities on the British Columbia coast, from Granby Bay to the Strait of Georgia and on the west coast of Vancouver Island, at depths from 42 to 108 fathoms. Thirteen specimens were attached to the shrimp *Pasiphaea pacifica* and the rest were loose among other animals in trawl catches. These specimens were compared with a syntype of *H. alaskensis* (Cat. no. 29250), and the holotype of *H. californiensis* (Cat. no. 38527), obtained on loan from the United States National Museum, Washington, D.C.

[1]Received for publication May 27, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

The purpose of this paper is to present a redescription of *H. alaskensis*, based on the original description, type specimens, and the additional material now at hand, and to propose that *Holophryxus californiensis* and *Hypodajus georgiensis* are synonyms of *Holophryxus alaskensis*. Specimens of *H. alaskensis* have been sent to the National Museum of Canada, Ottawa. Most drawings were made with the aid of a camera lucida.

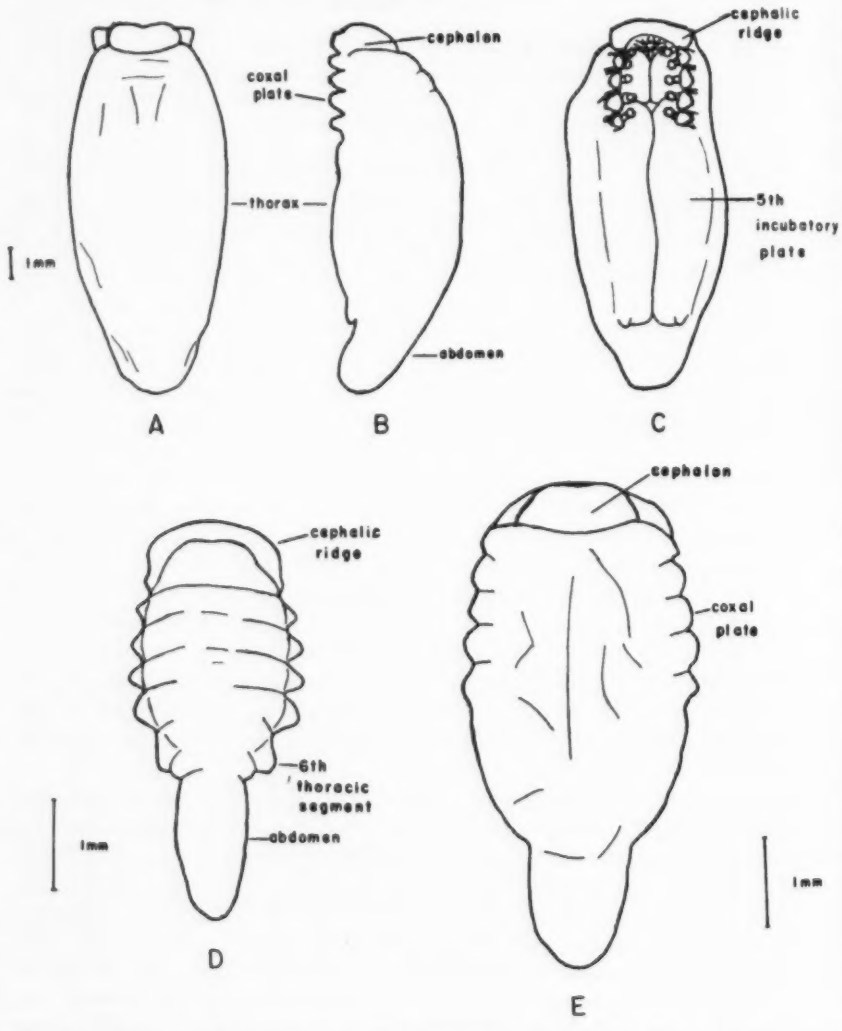


FIG. 1. *Holophryxus alaskensis*. Diagrams of females. (A) mature, dorsal view, (B) mature, lateral view, (C) mature, ventral view, (D) early immature, dorsal view, (E) later immature, dorsal view.

DESCRIPTION OF *HOLOPHRYXUS ALASKENSIS*

Holophryxus alaskensis Richardson, 1905a.
Holophryxus alaskensis Richardson, 1905b.
Holophryxus californiensis Richardson, 1908, 1909.
Hypodajus georgiensis Nierstrasz and Brender à Brandis, 1931.

MATURE FEMALE (Fig. 1 and 2).

Generally elongate and symmetrical but may be irregular in outline; dorsal surface convex, ventral concave.

Cephalon separate from thorax, hemispherical, in some specimens bilobed. Cephalon may be anterior in position and visible dorsally (Fig. 1A), or located more ventrally (Fig. 2B), in the case of a stouter and deeper body form. Cephalic ridge or lamella may be conspicuous or obscured. Eyes absent. Mandibles styliform, bordered by first antennae and maxilliped (Fig. 3B). First antennae rudimentary, flattened, tapering from lobate base to rounded end, 2 articles (?). Second antennae (Fig. 3D), short, thorn-like, tapering sharply, distal end slightly curved, arises adjacent to maxilliped, and lies closely to cephalic lamina, directed obliquely. Maxillipeds longer than first antennae, slightly flattened, digital, directed slightly obliquely, distal end rounded and meet in midline. Sternum soft plate, keel-like in position, lies between maxillipeds and first oostegite.

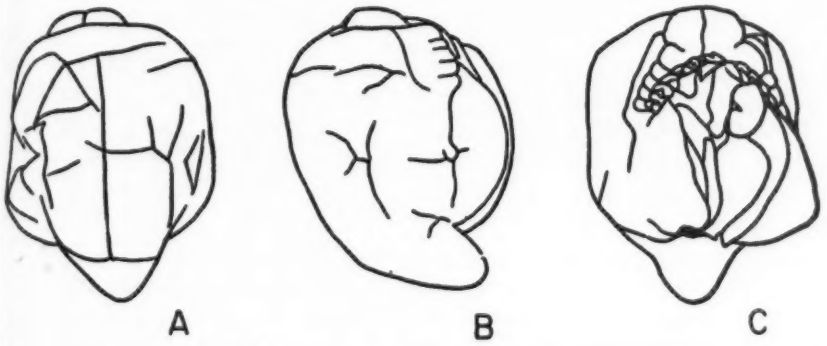


FIG. 2. *Holophryxus alaskensis*. Diagrams of mature female. (A) dorsal view, (B) lateral view, (C) ventral view. After Richardson, 1905a.

Segmentation of thorax shown generally only in lateral view (Fig. 1B) by 4 coxal plates. Folds in the integument may give impression of segmentation. Five pairs of pereiopods flanking oral region, with bases adjacent to coxal plates. Pereiopods prehensile (Fig. 3C), each with apparent fusing of propodus and carpus to form globular segment. Five pairs of incubatory plates (oostegites) arise from bases of pereiopods. First 4 pairs small; the first pair appears divided into 4 lobes, 2 lobes visible (Fig. 3B) posteriorly to maxillipeds, others hidden and one of these lies adjacent to sternum; and generally other 3 pairs hidden; fifth pair large with each basal part continuous with lateral margin of thorax, and extending to its posterior part. Each plate of fifth pair separated in midline by longitudinal slit, or overlapping slightly; when body form irregular these plates spread widely revealing the smaller plates underneath. Posterior margin of each fifth plate fringed with 10 slender flexible spines. Lateral margin of thorax ends with protuberance, a remnant of sixth coxal plate prominent in immature stages.

Abdomen projects beyond thorax as conical prominence, lacking segmentation and appendages.

Eighteen specimens examined: length 5.5–12.0 mm, width 2.5–6.0 mm. Colour in life, maize; in alcohol and formalin, yellowish white.

The female attaches itself to the dorsal surface of the carapace of the shrimp *Pasiphaea pacifica* with the cephalon directed posteriorly. On the carapace of one specimen of *P. pacifica* were found marks made by the mandibles and pereiopods of *H. alaskensis*. These marks are similar to those reported by Stephenson (1912) for the Atlantic species, *Holophryxus acanthephyrae*.

Immature Female (Fig. 1D, E).

Elongate and symmetrical. Cephalon anterior in position, prominent and slightly bilobed or somewhat flattened with rounded lamella. Eyes absent. Appendages in oral region as in mature females.

Segmentation of thorax shown in lateral and dorsal views (Fig. 1E) by 4 coxal plates; or by partial separation of 6 segments (Fig. 1D). Six pairs of prehensile pereiopods, 5 pairs together in anterior region of thorax and sixth pair located at posterior of thorax. In early stage (Fig. 1D) sixth pereiopods arise from segment showing slight divergence towards posterior; later, pereiopods and reduced coxal plates located adjacent to posterior margin of 5th incubatory plates. In later stage, 5 pairs of incubatory plates present and all visible in ventral view, separated widely in midline.

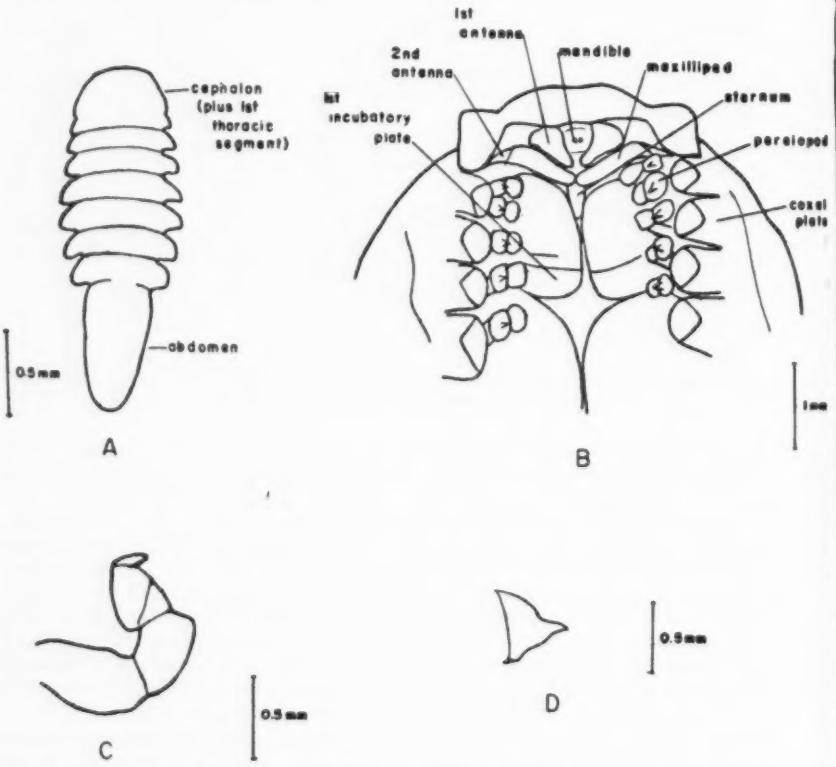


Fig. 3. *Holophryxus alaskensis*. (A) Male, dorsal view, (B) mature female, ventral view of oral region, (C) female, right 5th pereiopod, (D) female, second antenna.

Abdomen conical, tapering posteriorly, relatively longer than in mature females; lacks segmentation and appendages.

Two specimens examined: length 4.3 and 5.5 mm, width 2.0 and 2.6 mm. Colour in formalin, yellowish white.

One immature female was found on the ventral surface of the abdomen of the shrimp *Pasiphaea pacifica*, and the other was attached to the carapace of another shrimp of the same species.

MALE (Fig. 3A).

Elongate and symmetrical, dorsal surface slightly convex, ventral concave. Cephalon large and rounded anteriorly, and fused with first thoracic segment. Eyes absent. First antennae, with lobate base but no indication of flagellum. Second antennae elongate, extending posteriorly to about second thoracic segment, base with flagellum apparently without articulation. Mandibles styliform.

Five segments of thorax separated, sixth appears fused with abdomen. Segments subequal, lateral margins rounded, directed posteriorly. Seven pairs of prehensile pereiopods.

Abdomen unsegmented, elongate, round, tapering slightly to posterior, length less than 6 thoracic segments, no appendages.

Two specimens examined: length 1.9–6 mm, width 0.6–2 mm. Colour in formalin, yellowish white.

Males are found in the incubatory cavity of females having the symmetrical body form with the inner margins of the fifth incubatory plates close together. No male was found in females with the incubatory plates spread apart (Fig. 2C), or in an immature female having a gap between the small, undeveloped plates.

DISCUSSION

From comparisons of the present specimens with type specimens, it is concluded that *H. californiensis* is synonymous with H. *alaskensis*. The body shapes of the two forms differ somewhat, but anatomical features appear identical. Specimens designated as *H. californiensis* by Richardson were elongate and symmetrical, and the holotype was attached to *Pasiphaea pacifica*, whereas those described as *H. alaskensis* were fairly stout and irregular in body form, and were found without host shrimps. In the present collection those females found on *P. pacifica* were elongate also and the stout ones were unattached, although *P. pacifica* appeared in the same trawl catches. It is believed that the stout body form of the parasite is associated with the attainment of sexual maturity in female specimens. Mature females may be less able to adhere to their hosts, and become detached in a dredge or trawl.

The type specimens of *Hypodajus georgiensis* were not examined. The description by Nierstrasz and Brender à Brandis fits in most details the description of *Holophryxus alaskensis*, except that *Hypodajus georgiensis* was described as having segmentation of the thorax, and only 4 pairs of incubatory plates. The authors stated that segmentation was apparent only from faint grooves on the anterior dorsal part of the thorax. Similar grooves were found on several specimens of *Holophryxus alaskensis*, but they proved to be folds in the integument and not related to segmentation. In their count of the number of

oostegites Nierstrasz and Brender à Brandis were uncertain that the large ventral thoracic plates were to be included; however, these had been determined as the 5th oostegites by other workers (Richardson, 1905a, Stephensen, 1912). *Hypodajus georgiensis* was found on a pasiphaeid shrimp which in the Strait of Georgia (type locality) would almost certainly be *Pasiphaea pacifica*, the established host of *Holophryxus alaskensis*.

Thus, it appears reasonable, considering the above points, to conclude that *Hypodajus georgiensis* is a synonym of *Holophryxus alaskensis*. Also, it follows that the generic name *Hypodajus* must be considered as a synonym of *Holophryxus*. *H. alaskensis* remains as the type-species of the genus.

In the north Pacific region two closely related species, *H. giardi* Richardson 1908 and *H. fusiformis* Shiino 1937, have been described. The former was from the Bering Sea and the latter from the coast of Japan. *H. alaskensis* resembles *H. giardi* more closely but it lacks the conspicuous cephalic ridge of *H. giardi*. The female of *H. alaskensis* differs from that of *H. fusiformis* in having 5 pairs of incubatory plates instead of 4; the male of *H. alaskensis* lacks the squarish protuberance on the posterior margin of the abdomen.

Thus, with the proposed synonymy, the known distribution of *H. alaskensis* is from Behm Canal, Alaska, to Santa Barbara Channel, California, at 42–350 fathoms. The host, *P. pacifica*, is known to occur from Unalaska to the Gulf of California (Rathbun, 1904).

ACKNOWLEDGMENT

Dr L. Margolis kindly read the manuscript and offered valuable comments.

REFERENCES

NIERSTRASZ, H. F., AND G. A. BRENDER À BRANDIS. 1931. Papers from Dr Th. Mortensen's Pacific Expedition 1914–16. Epicaridea II. *Viden. Meddel. Dansk Naturhist. Foren. København*, **91**: 147–225.

RATHBUN, M. J. 1904. Decapod crustaceans of the northwest coast of North America. *Harriman Alaska Exped. Ser.*, **10**: 210 pp.

RICHARDSON, H. 1905a. Isopods of the Alaska Salmon Investigation. *Bull. U.S. Bureau Fish.*, **24**: 209–221.

1905b. A monograph on the isopods of North America. *Bull. U.S. Nat. Mus.*, **54**: 727 pp.

1908. On some isopods of the family Dajidae from the northwest Pacific Ocean, with descriptions of a new genus and two new species. *Proc. U.S. Nat. Mus.*, **33**: 689–696.

1909. Isopods collected in the northwest Pacific by the U.S. Bureau of Fisheries steamer *Albatross* in 1906. *Ibid.*, **37**: 75–129.

SHIINO, S. M. 1937. *Holophryxus fusiformis*, a new species of Dajidae, Epicaridea. *Annot. Zool. Jap.*, **16**(3): 188–191.

STEPHENSEN, K. 1912. Report on the Malacostraca collected by the *Tjalfe*-Expedition, under the direction of cand. mag. Ad. S. Jensen, especially at W. Greenland. *Vidensk. Meddel. naturh. Foren. København*, **64**: 57–134.

Problems in Zoogeography of the Lake Trout, *Salvelinus namaycush*[1]

By C. C. Lindsey

Institute of Fisheries, and Department of Zoology
University of British Columbia, Vancouver, B.C.

ABSTRACT

Disagreement exists in the literature as to whether lake trout survived Wisconsin glaciation north or south of the ice sheet. Other freshwater fishes whose range in North America equals or exceeds that of lake trout all survived in both northern and southern refugia. Arguments in favour of a southern refugium for lake trout include their wide distribution eastward to Nova Scotia and New England, their presence in some Mississippi headwaters, and possible late-Wisconsin date of a fossil lake trout south of glaciation. Absence from some habitable lakes along the southern margin of glaciation is attributable to northward shift of isotherms during the hypsithermal period. A northern refugium is suggested by occurrence of lake trout in remote parts of Alaska, and the improbability of their having failed to reach and persist in Alaska prior to last glacial advance. They do not now closely approach Bering Strait, and may be held in check by ecological factors which have been operative also during previous glacial and interglacial periods, on the Bering land bridge as well as on the continent. *Hucho taimen* is a related Asian counterpart whose dispersal may be similarly controlled. Large lampreys may prevent dispersal of lake trout into lower water courses and the sea.

INTRODUCTION

The lake trout, *Salvelinus namaycush* (Walbaum), poses a distributional problem unique among North American fishes. It is the only freshwater species that ranges into the far north of Canada and Alaska, but that does *not* extend westward across Bering Strait into Siberia. Since every other freshwater fish whose range approaches Bering Strait has succeeded in crossing over, why has the lake trout failed?

There is complete disagreement in the literature as to the late Pleistocene glacial refugium of the lake trout. Radforth (1944) believed the lake trout survived the last glaciation north of the ice sheet in Alaska, and has since spread south. Walters (1955) concluded that the lake trout did not survive in Alaska, but has spread from a refugium in the Mississippi valley. Wynne-Edwards believed in a southern refugium (1947, p. 19), with the possibility of a second refugium in the Yukon River basin (1952, p. 2).

This paper assembles the available evidence concerning lake trout zoogeography, and attempts to assess the conflicting hypotheses concerning where the lake trout originated and why it is confined to its present range.

[1]Received for publication May 13, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

PRESENT LAKE TROUT DISTRIBUTION

Figure 1 indicates distributional limits of the lake trout. Further details and comments are in the Appendix.

The present natural range of lake trout lies almost entirely within the limits of Pleistocene glaciation. South of the St. Lawrence–Great Lakes and Hudson Bay drainages they occur in Nova Scotia, New Brunswick, some headwater lakes of Atlantic drainages as far south as the Hudson River, in some Wisconsin and Minnesota lakes a few miles south of the Mississippi–Great Lakes divide and in the extreme northwestern headwaters of the Missouri River in Montana. West of the continental divide they are in the upper Fraser but not the Columbia, and in Pacific drainages north to Cook Inlet. They occur in Bristol Bay drainages. In the Yukon River they are present in headwater lakes but are apparently absent from the unglaciated middle and lower portions of the drainage basin. In northern Alaska they are also in higher ground along the Brooks Range, but not in coastal lowlands. Along the Canadian Arctic coast they extend out onto several islands of the Archipelago, and range eastward to Ungava and Labrador but do not reach Newfoundland.

South of their natural range, lake trout have been successfully planted (to establish self-sustaining populations) in New England and westward, including the Canadian prairie provinces, and in high lakes of some western States as far south as Nevada, California, and Colorado.

Lake trout are confined at their southern limits to deep cool lakes, but towards the north they occur also in shallower lakes and even in rivers. Although they are primarily lake spawners, stream spawning occurs in some tributaries to Lake Superior (Loftus, 1958) and may be commoner towards the north.

There are no records of lake trout from salt or brackish water in the southern portion of their range. However, like several other species ordinarily considered to be purely freshwater (e.g. grayling, *Thymallus arcticus*) they are sometimes encountered in brackish water in colder regions (see Appendix). Indeed, they must have crossed sea water to reach lakes on King William Island in the Canadian Arctic, for this island has risen from the sea only since disappearance of local glaciation (Wilson, 1958).

No geographically consistent divergence in morphology of lake trout is known. Local "races" may be recognized, based on colour differences, fatness, or growth rate, but these are sporadic in their distribution and have not provided evidence of genetically divergent stocks arising from separate glacial refugia. However, careful study on adequate material from over the range of the species has not yet been attempted.

REFUGIA OF OTHER WIDE-RANGING SPECIES

The glacial refugia for many northern fishes are evident from their present distributions. Some species, to judge by their absence from the Yukon River system today, obviously came from the south; others obviously came from the

north. A few (including the grayling, and the arctic chars, *Salvelinus alpinus* subspp.) survived both north and south of the ice sheet and have not rejoined their ranges since.

There remains a number of species widely distributed from the Great Lakes to Alaska and, except for the lake trout, across Bering Strait into Siberia. It is notable that every one of these species whose range surpasses that of the lake trout gives evidence of having survived in two or more glacial refugia, at least one south and one north of the ice sheet. Over the North American range of each, there occurs one large area repopulated by fish which have spread northward from south of glaciation, a second large area repopulated by a morphologically distinguishable type which has spread east and south from Alaska, and a zone of intergradation where the two types have met. Such a picture emerges for the slimy sculpin, *Cottus cognatus* (McAllister and Lindsey, 1961), the ninespine stickleback, *Pungitius pungitius* (McPhail, 1963a), perhaps the humpback whitefishes, *Coregonus* spp. (Lindsey, 1963, p. 765), and probably for at least four other species (McPhail, MS, 1963b).

Evidently no other freshwater fish which came from a single North American glacial refugium has achieved a postglacial distribution as wide as that now occupied by the lake trout. Therefore, to suppose that lake trout have reached New England, the upper Mississippi and upper Missouri from Alaska since glaciation (Radforth, 1944), or else have reached Bristol Bay drainages and the Arctic slope of Alaska from south of the ice (Walters, 1955), is to credit the lake trout with a unique feat of dispersal. Such a possibility cannot be altogether discounted, as the lake trout is well-adapted to capitalize on temporary lakes along the ice face as an avenue for rapid dispersal during waning glaciation.

HAD LAKE TROUT A SOUTHERN REFUGIUM?

The only recorded fossil lake trout comes from Wisconsin close to the southern edge of glaciation within the present Mississippi drainage, a short distance south of the present natural range of the species in the area (Fig. 1). The surrounding clay also contains elephant, mastodon and caribou remains. It was assigned to the interglacial period between the second and third Pleistocene glaciations by Hussakof (1916). Recently, however, radio carbon techniques give a much later date to the surrounding beds (12,500 to 16,000 B.P.), corresponding to the closing stages of the last or Wisconsin glaciation (R. F. Black, in correspondence to J. D. McPhail). If the later dating be accepted, it offers direct evidence of the presence of lake trout in a southern refugium during Wisconsin glaciation.

Lake trout now occur naturally in some lakes around the northern margin of the Mississippi watershed in Wisconsin and Minnesota. These records do not, however, constitute proof of a Mississippi refugium, because some of the divides between the Great Lakes and Mississippi basins in Wisconsin are low and swampy, and several species of fish have evidently crossed them comparatively recently (Greene, 1935). Such routes would be less suitable to lake trout than to warmer water species.

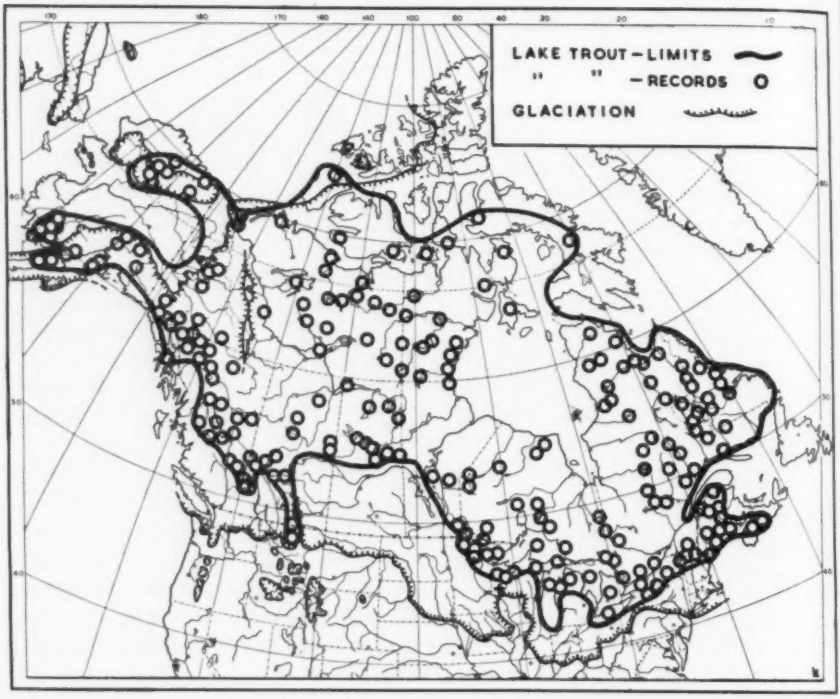


FIG. 1. Distribution of *Salvelinus namaycush*, based on data in the Appendix. Introductions by man not shown. Complete coverage attempted only for records lying close to margins of the range. Locality of fossil marked by cross. Limits of glaciation are for the last (Wisconsin) period (Wilson, 1958; Flint, 1945; Hopkins, 1959; Sachs and Strelkov, 1961) except for the western Brooks Range where glaciation limits shown are probably Illinoian.

Elsewhere in the Mississippi basin, natural populations of lake trout inhabit mountain lakes at the extreme headwaters of the Missouri River in northern Montana. These lakes lie immediately south of the Saskatchewan River basin, and might have received fishes from the north via drainage diversions associated with ice retreat. However, this area lies at the southern margin of continental glaciation. To suppose that lake trout entered the lakes in question from the Yukon basin, one must postulate that they did so by an ice-free corridor which would have had to connect the Yukon and present Saskatchewan River basins *before* drainage disruptions in Montana were complete. Such a corridor could conceivably have opened during a temporary drawing apart of the Cordilleran and Keewatin ice sheets; available geological evidence cannot decide this question.

A much simpler hypothesis is that lake trout existed throughout Wisconsin glaciation in Montana waters and elsewhere in the Mississippi basin, and moved northward following the retreating ice. The refugium in this area may have extended northward some distance into Alberta, where the edges of the Cordilleran and Keewatin ice sheets probably failed to meet (Heusser, 1956).

Regardless of possible origin of lake trout now in Montana, the presence of natural populations as far east as New England and Nova Scotia, coupled with the fossil of probably late Wisconsin age, strongly suggest one or several southern refugia. These may well have existed east as well as west of the Appalachians, wherever suitable lakes lay.

An objection to the foregoing hypothesis rises from the absence of natural lake trout populations in many lakes just south of their present range. Lake trout have been successfully established by artificial introductions in lakes north of the limits of glaciation but south of natural populations of the region (e.g. in New England, and southwestern Manitoba). If lake trout moved north following glaciation they must have passed across the lakes in question. Why then are they absent from these lakes, which we know to be capable of supporting lake trout?

The answer may lie in the "hypsithermal", or "altithermal", a period of thermal maximum which occurred between about 7000 and 4500 B.P.—that is, after retreat of the last glaciation (Antevs, 1953). During the hypsithermal, temperatures were higher than at present (about 1 C° yearly average), with accompanying northward shift of isotherms. After glacial retreat but before the hypsithermal, lake trout probably persisted farther south than at present, in many lakes including those into which they have recently been re-introduced. Their southern limit of distribution was probably determined largely by the combination of water temperature, depth, and bottom type required for successful reproduction (Royce, 1951). When temperatures rose during the hypsithermal, the ranges of many species shifted north; for example, pollen analysis shows that several species of trees extended their ranges farther north then than at present (Deevey, 1949). It is suggested that lake trout then died out in a number of marginal habitats along their southern limits. Since the hypsithermal, a somewhat cooler climate has rendered some of these waters again habitable, as demonstrated by successful southward introductions by man.

The absence of lake trout from Newfoundland is puzzling; if they persisted south of the ice sheet, they might be expected to have crossed from the lower St. Lawrence River to Newfoundland during ice retreat, when temperatures and salinities were low. Such sea crossings have been accomplished in the Canadian Arctic (for example to King William Island, which has emerged from the sea only comparatively recently). Perhaps lake trout did not reach the Gulf of St. Lawrence until after higher salinity and temperature obstructed the crossing. Postglacially an arm of the sea extended up the St. Lawrence Valley to Lake Ontario, and during that time an ice cap may have persisted in central Maine (Borns, 1963) perhaps blocking the northeastward spread of freshwater fishes. Lampreys may also have checked their eastward dispersal, as is discussed later.

Although lake trout probably had one or several southern refugia, they were almost certainly absent from the Pacific slope south of the ice sheet. None occur naturally in the Columbia River basin today. They have apparently reached the upper Fraser River and Pacific drainages farther north, by crossover from the east or north. One probable route was via postglacial Miette

Lake, which lay across the continental divide and connected Moose Lake at the head of the Fraser River to the Athabasca River basin which then drained south (Taylor, 1960).

HAD LAKE TROUT A NORTHERN REFUGIUM?

Lake trout are now distributed in a crescent bordering three sides of the unglaciated basin of the Yukon River (Fig. 1). They very probably survived the last glaciation in one or more areas of this Yukon refugium (as well as south of the ice sheet). Presumably lake trout were widespread in northern North America during the preceding interglacial period, particularly in cold regions, and it is difficult to postulate any sequence of events during the development of the last glaciation which would fail to leave populations somewhere in one or more northern refugia. Evidence has been presented above that several other species, probably no better adapted, survived in the north.

Apart from the unlikelihood of lake trout having been excluded from a northern refugium, the species is now distributed in parts of Alaska too remote to suggest postglacial dispersal from the Mississippi basin. It occurs in tributaries to Bristol Bay, in remote lakes tributary to the Kuskokwim River in the Kilbuck mountains, and in lakes on north and south slopes of the Brooks Range in northern Alaska. The possibility of lake trout having reached these places postglacially from a southern refugium cannot be ruled out, but it requires a feat of dispersal not accomplished by any other southern species. The two known southern invaders of the Yukon River system are the lake chub, *Couesius plumbeus*, and the trout-perch, *Percopsis omiscomaycus*. The former have been taken downstream on the Yukon River only as far as Nulato (BC 60-367), and the latter at Andreafsky (BC 60-390); both are apparently absent from all Alaskan drainages other than the Yukon River. Present Alaskan lake trout distribution suggests not a recent and expanding invasion from the south, but rather the somewhat disjunct and almost relict distribution of a long-established species.

The discontinuity of the lake trout in Alaska is striking. It results at least in part from the discontinuity of suitable habitats. No records exist of lake trout in or near almost the whole of the muddy mainstem of the Yukon River in Alaska, although the species abounds in large clear lakes in the Canadian headwaters. Precipitation in this area is low (presumably a cause of non-glaciation during the Pleistocene) and much of the region traversed by the river is quite dry. More important, deep or moderate lakes are abundant in glaciated areas, but are strikingly rare in unglaciated portions of the Yukon basin. Apparently suitable waters of the Seward Peninsula adjoining Bering Strait probably do not contain the species (but see Appendix); these are separated from the nearest lake trout populations to the east by lowland tundra areas.

A strong argument has been put forward by Walters (1955) against lake trout having been present in the Yukon refugium during glaciation, in that had the species been there it would have crossed the Bering land bridge into Siberia. During the maximum glaciation so much water was locked up in ice sheets that the sea level dropped, and a strip of land over 1000 miles from north to south

was exposed, connecting Alaska and Siberia (Hopkins, 1959). Every freshwater fish species which now reaches Bering Strait from either side has crossed over. Direct evidence of at least three of these having used the land bridge is found on St. Lawrence Island, which lies south of Bering Strait and represents the highest part of the drowned bridge. On it now occur the arctic grayling, the Alaska blackfish, *Dallia pectoralis*, and the slimy sculpin, *Cottus cognatus*. All are freshwater forms which, although they may venture into brackish water, have not likely crossed 40 miles of sea to the nearest land in Siberia. These and other fish must have passed along from watercourse to watercourse which drained the land bridge during its emergence.

However, unlike these other species, lake trout do not now reach the Bering Strait. Their closest known approach is in the Kobuk River some 400 miles to the east. Whatever combination of factors now checks their westward expansion may very well have checked them also during emergence of the land bridge. If failure of lake trout to cross to Siberia be attributed solely to their absence from Alaska during the last glaciation, then one must suppose that they were also absent during every one of the preceding glaciations, when bridges existed. More probably, lake trout have survived in the Yukon River basin throughout several glacial and interglacial periods, but have rarely or never ranged westward as far as Bering Strait. Absence of suitable waters, particularly for reproduction, would be no less effective a barrier during glacial times than they are now.

If lake trout did occasionally reach the land bridge, they would probably have found it unsuitable for reproduction although perhaps not for survival. The whole of the drowned bridge is now very flat, and presumably it carried no deep lakes, but only meandering streams with gentle gradients and muddy bottoms. The bridge supported no forest, only tundra (Hopkins, 1959). On the Siberian side the Chukotsk Peninsula contains terrain and lakes which might be considered as suitable lake trout habitat. However, almost all of this was covered by an ice cap during the maximum (Illinoian?) glaciation, and at least part of the Chukotsk highlands were glaciated during the Wisconsin (Fig. 1) (Sachs and Strelkov, 1961). In the south, spawning lake trout require clean gravel or rubble bottom free of sand or mud, in lakes of suitable depths (Royce, 1951). Little is known of their spawning requirements in the north, but it may be surmised that conditions along the bridge, while allowing passage of suckers, graylings etc., were less favourable for the spread of lake trout.

Lake trout may have survived in northern refugia other than the Yukon River basin. Portions of the Bristol Bay drainage, and also the Arctic slope of Alaska north of the Brooks Range, were unglaciated. Several areas bordering the Gulf of Alaska may have escaped Wisconsin glaciation and could have served as refugia (Ferrians and Schmoll, 1957; Heusser, 1960; Karlstrom, 1961). The northwestern half of Banks Island in the Canadian Archipelago was unglaciated (Wilson, 1958). These areas now contain lake trout, and all might have contained them during Wisconsin times. Nunataks existed between the Cordilleran and Keewatin ice sheets in the Northwest Territories and perhaps farther south (Wilson, 1958); these were possibly refugia for some hardy plants and animals, but probably not for fishes.

ASIAN COUNTERPARTS

The lake trout is the most distinctive of the chars (genus *Salvelinus*), both in habits and structure (Rounsefell, 1958, 1962; Morton and Miller, 1954), so much so that strong arguments have been advanced for its placement in a separate genus *Cristivomer* (Vladykov, 1954). Since no obviously close relative of *S. namaycush* survives, it may be profitable to look outside the genus for clues as to its ancestry, and hence to its distributional history.

There occur in north Asia two genera of salmonids which in some ways suggest counterparts of the lake trout. The lenok, *Brachymystax lenok*, is a large river-dwelling species which never descends to the sea (Berg, 1948). Its range extends across northern Russia from the Ural Mountains eastwards to within 600 miles of the Bering Strait in the Kolyma River basin. However, in its rather small mouth and skull morphology the lenok somewhat resembles the grayling *Thymallus* (Norden, 1961), and is apparently not very closely related to the lake trout.

The other genus of strictly freshwater Eurasian salmonids is *Hucho*, with four species which range from the Danube to Siberia and south to Japan; of these the taimen, *Hucho taimen*, occurs in the Volga and in Russian Arctic drainages from the Pechora River eastward to within 1000 miles of Bering Strait in the Indigirka River (Fig. 2). It lives either in rivers or in lakes, and never descends to the sea (Berg, 1948). Like the lake trout, it reaches a large size.

Hucho taimen is without doubt a species perfectly distinct from *Salvelinus namaycush*, but the genera *Hucho* and *Salvelinus* do not differ sharply. Berg (1948) characterizes the genus *Hucho* as lacking teeth on the copulae (i.e. lacking basibranchial, or "hyoid", teeth). Norden (1961) omits this character in his summary of generic characters, for he found that although basibranchial teeth were lacking in *H. hucho* they were well developed in *H. perryi*. The lake trout always has several rows of strong basibranchial teeth. The arctic char, *S. alpinus*, has variable basibranchial teeth (McPhail, 1961), while other species of *Salvelinus* have these teeth weaker and less numerous, or absent (Morton and Miller, 1954). The character most often cited as diagnostic between *Hucho* and *Salvelinus*, the presence or absence of a gap between the palatine and vomerine teeth, is also unreliable. McPhail (1961) describes these teeth in *S. malma* as "sometimes continuous, usually not"; in *S. alpinus* Walters (1953) illustrates some specimens with continuous tooth rows and some without.

The principal remaining osteological differences between the genera, the proportions of the supraethmoid and the development of the ascending process of the premaxilla (Norden, 1961) are matters of degree only. In several osteological characters *Hucho* shows close relationship to *Salvelinus* (e.g. boat-shaped vomer, two parallel rows of strong teeth on the tongue), often with suggestions of closest relationship to *S. namaycush*.

Arguments based on other types of evidence can also be advanced to indicate that *S. namaycush* is the closest relative, amongst North American chars, to the

Eurasian *Hucho*. The lake trout has a remarkably large number of pyloric caeca (94–170, in contrast to less than 75 in other North American chars (Morton and Miller, 1954; McPhail, 1961)); so do species of *Hucho*, with 150–250 caeca, many more than in other Eurasian salmonids (Berg, 1948). Another feature shown graphically by Morton and Miller (1954) to characterize the lake trout is the placement of the dorsal fin relatively far back on the body. Measurements of photographs and drawings show that the taimen also displays this backward position in the dorsal fin. Size also has been mentioned; the lake trout is the largest species of *Salvelinus* (over 100 lb, 45 kg); *Hucho taimen* is even larger, up to 176 lb (80 kg) (Berg, 1948).

Salvelinus and *Hucho* differ in colouration, but again the lake trout shows some intermediacy. All *Salvelinus* have light markings on a darker background. All species in the genus other than *S. namaycush* have vivid coloured spots, at least at spawning time, and then the sides may become bright orange or red. Lake trout never have vivid coloured spots; their nuptial colouration may consist of a yellowish or light orange wash. *Hucho* has no light markings, but small black speckles which may vanish with age (Seeley, 1886). Like the lake trout, they lack bright coloured spots, but the body may become copper-red during spawning (Berg, 1948).

All species of *Salvelinus* spawn in autumn, but all species of *Hucho* spawn in spring, evidently in running water (Berg, 1948).

According to the phyletic tree suggested by Norden, the most primitive genus of salmonine fishes (and the closest to *Thymallus*) is *Brachymystax*, followed progressively by *Hucho*, then *Salvelinus*, then *Salmo*, and finally *Oncorhynchus*. From the evidence given above, the most "*Hucho*-like", (and hence presumably most primitive) species of *Salvelinus* is *S. namaycush*.

The generic distinction between *Hucho* and *Salvelinus* may be questioned. But so may the distinction between *Salvelinus* and *Salmo* (see particularly the autumn-spawning *Salmo trutta* with pale haloes), or the distinction between *Salmo* and *Oncorhynchus* (bridged by the trout-like *Oncorhynchus masou*). In the interests of stability, generic distinctions in this (or any other) family should not be tampered with unless *all* known species are carefully reviewed.

In summary, the taimen and the lake trout are both largely cold-adapted, almost purely freshwater species, evidently shunning lowland areas, each confined to one continent and approaching but not reaching Bering Strait (Fig. 2). The taimen spawns in spring, lives primarily in rivers and has dark speckling; the lake trout spawns in autumn, lives primarily in lakes and has pale markings. The two do not differ strikingly in morphology.

It is suggested that *Hucho* and *S. namaycush* may have had a common ancestor which crossed the Bering gap in early Pleistocene or pre-Pleistocene times. (The ancestor might have resembled *Hucho perryi*, which is char-like in possessing basibranchial teeth, and which evidently tolerates sea water (Berg, 1948).) Although they have diverged since, *H. taimen* and *S. namaycush* have apparently been subject to somewhat the same checks to geographic expansion

FIG. 2. Distribution of *Salvelinus namaycush* (hatched area) in North America, and of the genus *Hucho* in Asia. Stippled area – *Hucho taimen*. Circled areas: *H. i.* – *Hucho ishikawai*; *H. p.* – *Hucho perryi*. A fourth species, *Hucho hucho*, occurs in the Danube basin (*Hucho* distributions from Berg, 1948).

LAMPREYS AND LAKE TROUT DISTRIBUTION

A further clue to lake trout distribution may be found by examining the North American distribution of large predatory lampreys. These are, on the Atlantic coast, *Petromyzon marinus*, on the Pacific coast, *Entosphenus tridentatus*, and in Bering Sea and part of the Arctic Ocean, *Entosphenus japonicus* (probably synonymous with *E. lamottei*). The combined ranges of these, and the range of lake trout, are almost mutually exclusive (Fig. 3). *E. tridentatus* occupies the lower parts of the Fraser River system, lake trout the upper. *E. lamottei* runs up the Yukon River to Dawson City, while lake trout occupy only the headwaters above there. In the St. Lawrence River system lampreys were formerly confined to below Niagara Falls; their entry into the upper Great Lakes has caused a catastrophic decline in lake trout there (Eschmeyer, 1957).

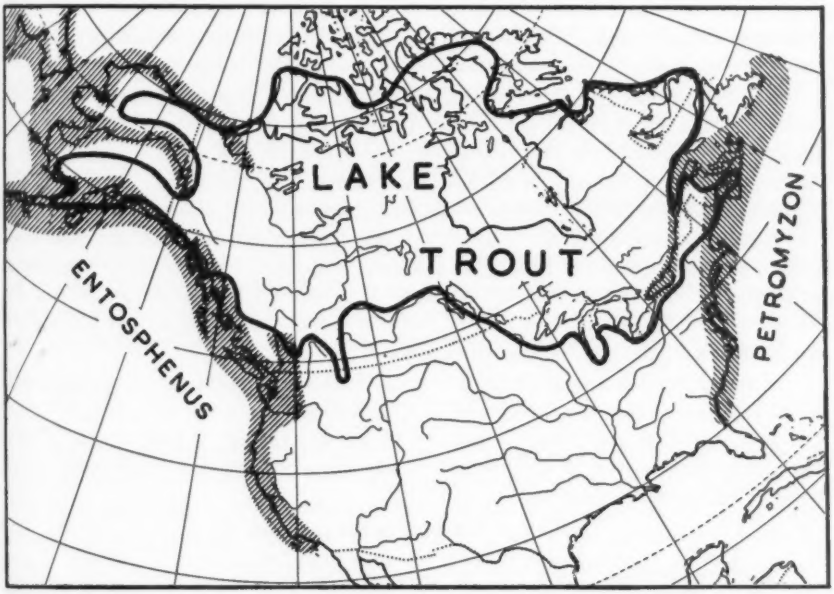


FIG. 3. Distribution of *Salvelinus namaycush* (heavy outline), and of large lampreys (hatched area). Limits of *Petromyzon* (before entry to upper Great Lakes) from Bigelow and Schroeder (1948).

Lake trout have not crossed narrow seas to Newfoundland, to Vancouver Island, or the Queen Charlotte Islands; nor have they crossed Bering Strait. All these marine waters contain predatory lampreys. In contrast, lake trout *have* crossed the sea to reach Banks, Victoria, King William, Southampton, and other Arctic islands, all probably beyond the range of marine lampreys. (Exceptionally, lake trout have apparently crossed a narrow stretch of sea to reach Admiralty Island in southeastern Alaska, within the range of *E. tridentatus*.)

These phenomena may arise from the higher sea temperatures and salinities existing towards the south, but presumably during ice recession even the more southern sea channels contained relatively cold brackish water.

Lake trout and large lampreys do overlap in a few localities. Lake Ontario contained *Petromyzon* and yet supported a moderate lake trout fishery (Dymond, 1928) but these lampreys evidently did not migrate to sea, and were smaller than the marine form (Bigelow and Schroeder, 1948). Cayuga Lake in New York contains both species, but here the lampreys are a somewhat dwarfed landlocked race (Wigley, 1959). In British Columbia a few sea-run *Entosphenus tridentatus* enter Shuswap Lake which also has lake trout. The Naknek River system tributary to Bristol Bay has lake trout and sea-run lampreys. Great Slave Lake contains many lake trout and a few *E. lamottei* (Rawson, 1951), but the latter are non-migratory and much smaller than their Bering Sea counterparts. Several species of lampreys other than those named share lake trout waters in the southeast, but these are either non-parasitic or are smaller than the sea-running species, and presumably do not pose a serious threat.

Experience in the Great Lakes shows that lake trout are peculiarly sensitive to lamprey attack, due perhaps to their behaviour or to their life history. There they have been decimated by lampreys (Eschmeyer, 1957), while other salmonid species (including the introduced *Salmo gairdnerii*) have been less affected. It is suggested that the lake trout has evolved in areas of North America not occupied by large predatory lampreys. Long exposure to lampreys in a few areas such as Lake Ontario may have produced by selection local races better able to withstand predation. The recent striking decrease of lake trout formerly protected by Niagara Falls may be due in part to the very long immunity which lake trout stocks had enjoyed in the upper Great Lakes.

The impact of lampreys on lake trout distribution should not be over-stressed, for the subject is highly conjectural. Lampreys are certainly not claimed to be the only, nor even the prime factor in limiting the spread of lake trout. They may, however, be one of the factors which have combined to hold lake trout within their present confines.

CONCLUSIONS

Radforth (1944) argued against the lake trout having survived south of the ice sheet, due to the absence of suitable habitats there. However, even now there are natural lake trout populations close to the southern edge of glaciation; at lower temperatures and with melt-water coming from the ice face, suitable environments were almost certainly present. The eastward distribution as far as New England and Nova Scotia suggests one or more southern refugia. The existence of a fossil in Wisconsin shows that the species was certainly present at some time south of the glaciated area; the most recent dating of the adjoining beds indicates that the specimen lived there about the time the last ice sheet was beginning to wane. Absence of lake trout from some suitable lakes along the southern margin of glaciation may be explained by failure to reproduce there during a post-glacial "hypsithermal" period.

Walters (1955) argued against the lake trout having survived north of the ice sheet due to its absence from Siberia. However, even now the lake trout is absent from areas close to Bering Strait. Whatever conditions now prevent it from expanding towards the Strait may very well have been operative throughout previous glacial and interglacial periods. Its wide but scattered Alaskan distribution does not suggest that it is a post-glacial immigrant which will shortly expand westward to the Strait. If indeed it has penetrated from the Mississippi to remote western and northern Alaskan areas in recent times, there seems no reason why it should have failed to reach Alaska and become established there during previous interglacial periods. More likely it, and perhaps its relatives *Hucho* and *Brachymystax*, have survived in the north for a long time, but have failed to reach and cross the Bering area for ecological reasons. These may include the absence of lakes with suitable spawning sites in unglaciated regions circumscribing their present range, the barriers of silt and shallow water in lowland areas (including fresh waters of the land bridge while it was emergent), and blockage of suitable habitats by local ice in the Chukotsk highlands at times when a land bridge existed. Higher sea temperatures and salinities are now a further discouragement to crossing Bering Strait. Another factor which may hold the lake trout in check is the presence of predatory anadromous lampreys in the lower reaches of all but Arctic Ocean drainages.

The lake trout is a distinctive species, which has probably existed in northern North America for a long time. During the last, and perhaps during earlier glaciations, it probably survived in several refugia, some north and some south of the ice sheet. Morphological or physiological differences, such as occur in several other species, may yet be found which will enable us to distinguish between populations originating from the different refugia.

ACKNOWLEDGMENTS

For information, records, or specimens, I am grateful to the following persons: Dr J. A. Elson, Dr F. H. Fay, Dr S. Y. Koo, Mr J. S. Nelson, Mr K. E. Northcote, Mr Dean Paddock, Dr S. Pennoyer, and Dr W. B. Scott. Dr J. D. McPhail helped collect many of the specimens of lake trout and other species recorded here. Dr T. G. Northcote and Dr N. J. Wilimovsky made useful criticisms of the manuscript.

REFERENCES

ANDERSON, R. M. 1913. Report on the natural history collections of the expedition. Fishes, pp. 450–455. *In* V. Stefansson, My life with the eskimo. Macmillan Co., New York.

ANTEVS, E. 1953. Geochronology of the deglacial and neothermal ages. *J. Geol.*, **61**: 195–230.

BERG, L. S. 1948. (Freshwater fishes of the U.S.S.R. and adjacent countries. Vol. 1.) Ed. 4, *Zool. Inst. Akad. Nauk SSSR*, **1**(27). (English translation, 1962. Office of Technical Services, OTS 61–31218, U.S. Dept. Commerce, Washington.).

BIGELOW, H. B., AND W. C. SCHROEDER. 1948. Cyclostomes. *In* Fishes of the western North Atlantic. Mem. Sears Foundation Mar. Res., No. 1, Pt. 1, pp. 29–58.

BORNS, H. W. 1963. Preliminary report on the age and distribution of the late Pleistocene ice in north central Maine. *Amer. J. Science*, **261**(8): 738–740.

CARL, G. C., W. A. CLEMENS AND C. C. LINDSEY. 1959. The fresh-water fishes of British Columbia. *British Columbia Prov. Mus., Handbook* No. 5, 3rd ed., 192 pp.

CLEMENS, W. A., R. V. BOUGHTON AND J. A. RATTENBURY. 1945. A preliminary report on a fishery survey of Teslin Lake, British Columbia. *Rept. British Columbia Dept. Fish.* for 1944, pp. 70–75.

CUERRIER, J.-P. 1954. The history of Lake Minnewanka with reference to the reaction of lake trout to artificial changes in environment. *Canadian Fish Culturist*, **15**: 1–9.

DEEVEY, E. S. 1949. Pleistocene research. 3. Biogeography of the Pleistocene. Pt. 1. Europe and North America. *Bull. Geol. Soc. Amer.*, **60**(9): 1315–1416.

DUFRESNE, F. 1946. Alaska's animals and fishes. A. S. Barnes and Co., New York, 297 pp.

DYMOND, J. R. 1928. Some factors affecting the production of lake trout (*Cristivomer namaycush*) in Lake Ontario. *Univ. Toronto Stud., Biol. Ser.*, No. 31; *Publ. Ontario Fish Res. Lab.*, No. 33, pp. 27–41.

EDDY, S., AND T. SURBER. 1947. Northern fishes with special reference to the Upper Mississippi Valley. Charles T. Branford Co., Newton Centre, Mass. (Revised edition) 276 pp.

ELLIS, D. V. 1962. Observations on the distribution and ecology of some Arctic fish. *Arctic*, **15**(3): 179–189.

ESCHMEYER, P. H. 1957. The near extinction of lake trout in Lake Michigan. *Trans. Amer. Fish. Soc.*, **85**(1955): 102–119.

EVERMANN, B. W., AND E. L. GOLDSBOROUGH. 1907. The fishes of Alaska. *Bull. U.S. Bur. Fish.*, **26**(1906): 219–360.

FERRIANS, O. J., AND H. R. SCHMOLL. 1957. Extensive proglacial lake of Wisconsin age in the Copper River basin, Alaska. (Abstract). *Bull. Geol. Soc. Amer.*, **68**: 1726.

FLINT, R. F. 1945. Glacial map of North America. Geol. Soc. Amer., Spec. Pap. 60, Part I (map, in 2 halves).

GREELEY, J. R., AND S. C. BISHOP. 1933. Fishes of the Upper Hudson watershed with annotated list. *In* A biological survey of the Upper Hudson watershed. Suppl. 22nd Ann. Rept. N.Y. State Cons. Dept., 1932, pp. 64–101.

GREENBANK, J. 1954. Sports fisheries survey, Katmai National Monument. Admin. Rept., U.S. Dept. Interior, National Parks Service, 31 pp.

GREENE, W. C. 1935. The distribution of Wisconsin fishes. Wisconsin Conservation Comm., Madison, 235 pp.

HARPER, F. 1961. Field and historical notes on fresh-water fishes of the Ungava Peninsula and on certain marine fishes of the north shore of the Gulf of St. Lawrence. *J. Elisha Mitchell Scientific Soc.*, **77**(2): 312–342.

HENSHALL, J. A. 1907. Culture of the Montana grayling. *Rept. U.S. Comm. Fisheries* for 1906, Doc. 628, 7 pp.

HEUSSER, C. J. 1956. Postglacial environments in the Canadian Rocky Mountains. *Ecol. Monogr.*, **26**: 263–302.

1960. Late-Pleistocene environments of North Pacific North America. *Amer. Geograph. Soc., Spec. Publ.* 35, 308 pp.

HINKS, D. 1957. The fishes of Manitoba. (Reprinted, with Supplement by J. J. Keleher and B. Kooyman). Manitoba Dept. Mines and Natural Resources, Winnipeg, 117 pp.

HOPKINS, D. M. 1959. Cenozoic history of the Bering land bridge. *Science*, **129**(3362): 1519–1528.

HUBBS, C. L., AND K. F. LAGLER. 1958. Fishes of the Great Lakes region. *Cranbrook Inst. Sci., Bull.* No. 26 (revised), 213 pp.

HUSSAKOF, L. 1916. Discovery of the Great Lake trout, *Cristivomer namaycush*, in the Pleistocene of Wisconsin. *J. Geol.*, **24**: 685–689.

KARLSTROM, T. V. 1961. Pleistocene physical and biological environments of Pacific South-central and Southwestern Alaska, Vol. 2, p. 895. (Abstract.) *In* G. O. Raasch, (ed.) Geology of the Arctic. Alberta Society Petroleum Geologists, Intern. Symp. No. 1, Univ. Toronto Press.

KENDALL, W. C. 1914. The fishes of New England. The salmon family. Pt. 1 — The trout or charrs. *Mem. Boston Soc. Nat. Hist.*, **8**(1): 1–103.

LINDSEY, C. C. 1963. Sympatric occurrence of two species of humpback whitefish in Squanga Lake, Yukon Territory. *J. Fish. Res. Bd. Canada*, **20**(3): 749–767.

LIVINGSTONE, D. A. 1951. The fresh water fishes of Nova Scotia. *Proc. Nova Scotian Inst. Sci.*, **23**(1): 1–90.

LOFTUS, K. H. 1958. Studies on river-spawning populations of lake trout in eastern Lake Superior. *Trans. Amer. Fish. Soc.*, **87**(1957): 259–277.

MACDONALD, W. H. 1951. Fishing in Alberta. Alberta Travel Bureau, Dept. Economic Affairs. A. Shnitka, Edmonton. 36 pp.

MANNING, T. H. 1943. Notes on some fish of the eastern Canadian Arctic. *Canadian Field-Naturalist* for 1942, **56**: 128–129.

1953. Notes on the fish of Banks Island. *Arctic*, **6**(4): 276–277.

MCALLISTER, D. E., AND C. C. LINDSEY. 1961. Systematics of the freshwater sculpins (*Cottus*) of British Columbia. *Bull. Nat. Mus. Canada*, No. 172, pp. 66–89.

MCPHAIL, J. D. 1961. A systematic study of the *Salvelinus alpinus* complex in North America. *J. Fish. Res. Bd. Canada*, **18**(5): 793–816.

1963a. Geographic variation in North American ninespine sticklebacks, *Pungitius pungitius*. *Ibid.*, **20**(1): 27–44.

MS, 1963b. The post-glacial dispersal of freshwater fishes in Northern North America. Ph.D. Thesis, Dept. Zoology, McGill University, Montreal, 167 pp.

MORTON, W. M., AND R. R. MILLER. 1954. Systematic position of the lake trout, *Salvelinus namaycush*. *Copeia*, 1954(2): 116–124.

NORDEN, C. R. 1961. Comparative osteology of representative salmonid fishes, with particular reference to the grayling (*Thymallus arcticus*) and its phylogeny. *J. Fish. Res. Bd. Canada*, **18**(5): 679–791.

PFAFF, J. R. 1937. Fishes, pp. 1–19, Vol. 2, No. 7. *In* K. Rasmussen, (ed.) Report of the fifth Thule expedition, Copenhagen.

RADFORTH, I. 1944. Some considerations on the distribution of fishes in Ontario. *Contr. Roy. Ontario Mus. Zool.*, No. 25, 116 pp.

RAWSON, D. S. 1951. Studies of the fish of Great Slave Lake. *J. Fish. Res. Bd. Canada*, 8(4): 207–240.

1961. The lake trout of Lac la Ronge, Saskatchewan. *J. Fish. Res. Bd. Canada*, **18**(3): 423–462.

ROUNSEFELL, G. A. 1958. Anadromy in North American Salmonidae. *U.S. Fish Wildlife Serv., Fishery Bull.*, **58**(131): 171–185.

1962. Relationships among North American Salmonidae. *Ibid.*, **62**(209): 235–270.

ROYCE, W. F. 1951. Breeding habits of lake trout in New York. *U.S. Fish Wildlife Serv., Fishery Bull.*, **52**(59): 59–76.

SACHS, V. N., AND S. A. STRELKOV. 1961. Mesozoic and Cenozoic of the Soviet Arctic, vol. 1, pp. 48–67. *In* G. O. Raasch, (ed.) Geology of the Arctic. Alberta Society Petroleum Geologists, Intern. Symp. No. 1, Univ. Toronto Press.

SCHULTZ, L. P. 1941. Fishes of Glacier National Park, Montana. *U.S. Dept. Interior, Nat. Park Serv., Conserv. Bull.* No. 22, 42 pp.

SCOTT, W. B., AND E. J. CROSSMAN. 1959. The freshwater fishes of New Brunswick: a check-list with distributional data. *Contr. Roy. Ontario Mus., Div. Zool. Palaeontology*, No. 51, 37 pp.

SEELEY, H. G. 1886. The freshwater fishes of Europe. Cassell and Co., London, 444 pp.

TAYLOR, R. S. 1960. Some Pleistocene lakes of northern Alberta and adjacent areas (revised). *J. Alberta Soc. Petroleum Geologists*, **8**(6): 167–185.

TOWNSEND, C. H. 1887. Notes on the natural history and ethnology of northern Alaska. *In* Capt. M. A. Healy, Report of the cruise of the Revenue Marine Steamer Corwin in the Arctic Ocean in the year 1885. House Exec. Doc. 153, 49th Congress, 1st Session, Vol. 32, pp. 81–102.

VLADYKOV, V. D. 1954. Taxonomic characters of the North American chars (*Salvelinus* and *Cristivomer*). *J. Fish. Res. Bd. Canada*, **11**(6): 904–932.

WALTERS, V. 1953. The fishes collected by the Canadian Arctic expedition, 1913–18, with additional notes on the ichthyofauna of western Arctic Canada. *Bull. Nat. Mus. Canada*, **128**: 257–274.

1955. Fishes of western Arctic America and eastern Arctic Siberia. *Bull. Amer. Mus. Nat. Hist.*, **106**(5): 255–368.

WEED, A. C. 1934. Notes on the sea trouts of Labrador. *Copeia*, 1934(3): 127.

WIGLEY, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. *U.S. Fish Wildlife Serv., Fishery Bull.*, **59**(154): 561–617.

WILSON, J. T. (Chairman) 1958. Glacial map of Canada. Geological Association of Canada, Ottawa.

WYNNE-EDWARDS, V. C. 1947. The Yukon Territory, pp. 6–30. *In* V. C. Wynne-Edwards, North West Canadian fisheries surveys in 1944–1945. *Bull. Fish. Res. Bd. Canada*, No. 72.

1952. Freshwater vertebrates of the Arctic and Subarctic. *Bull. Fish. Res. Bd. Canada*, No. 94, 28 pp.

APPENDIX

Sources of Locality Records of *Salvelinus namaycush*

Only references and collection numbers useful in defining the margins of the range are given. Most references give more detailed locality information than is listed below. Records refer only to natural occurrences unless otherwise specified. Areas are listed clockwise starting at the St. Lawrence River mouth. (Museum specimen numbers: BC — University of British Columbia; ROM — Royal Ontario Museum; SU — Stanford University).

South shore Gulf of St. Lawrence: in Restigouche River system; absent from Miramichi River system (where *Petromyzon* common) (Scott and Crossman, 1959).

Nova Scotia: various deep-water lakes in central area (Livingstone, 1951).

New Brunswick: St. John River headwaters (*Petromyzon* is absent above Grand Falls); St. Croix River headwaters; some isolated lakes in southwestern New Brunswick (Scott and Crossman, 1959).

Penobscot, Kennebec and Androscoggin River systems in Maine; upper Connecticut River system in northern New Hampshire and Vermont (Kendall, 1914).

Introduced as far south as Connecticut State (Hubbs and Lagler, 1958).

Upper Hudson River system in New York State (no *Petromyzon* reported) (Greeley and Bishop, 1933).

Lakes of Lake Ontario drainage in New York State; the main lakes of the Great Lakes basin (Hubbs and Lagler, 1958). Sea-run *Petromyzon marinus* ascend 40–50 miles above Quebec City (Bigelow and Schroeder, 1948); a smaller non-anadromous form occurs in Lake Ontario, but the species was formerly restricted to below Niagara Falls; a dwarf form occupies Finger Lakes of New York (Wigley, 1959).

A few deep lakes in northern Wisconsin and in the upper Peninsula of Michigan (Lake Superior drainage); in Mississippi River system, in central Wisconsin in 3 lakes within 15 miles of Great Lakes–Mississippi divide, and in western Wisconsin in 2 lakes within 25 miles of divide; some present watershed divides have altered even in historic times (Greene, 1935).

Fossil lake trout (skull bones of fish 2 ft long) in clay bed, Menominee, Dunn County, valley of Red Cedar River, 55 miles east of St. Paul, Minnesota (Hussakof, 1916).

In 5 northeastern counties of Minnesota, including at least one lake (Pikegama Lake near Grand Rapids) 20 miles within the Mississippi River drainage (Eddy and Surber, 1947).

Rainy River–Nelson River system in Ontario (Radforth, 1944).

Manitoba, in West Hawk Lake and other lakes of Whiteshell area northwest of Lake of the Woods; region east of Lake Winnipeg; occasionally in northern part of Lake Winnipeg; most of area north of 54° (Hinks, 1957).

Introduced to several Manitoba lakes in the Porcupine Mountain, Duck Mountain and Riding Mountain areas all west of Lakes Winnipegosis and Manitoba (Hinks, 1957). From available topographic maps, none of these lakes appears ever to have been part of glacial Lake Agassiz (J. A. Elson, personal communication).

Saskatchewan, in most deep lakes on Precambrian Shield, and north of 55°; between 54° and 55°, in 5 lakes tributary to Saskatchewan River and in 6 lakes tributary to Churchill River, including Cold Lake on Alberta border (Rawson, 1961).

Headwaters of Missouri River in Montana: Lower Two Medicine Lake (Schultz, 1941), and Elk Lake (Henshall, 1907).

Headwaters of South Saskatchewan River: in St. Mary, Crossley, and Glenns Lakes (Montana — Schultz, 1941), and in Waterton and Minnewanka Lakes (Alberta — Cuerrier, 1954).

Headwaters of North Saskatchewan River: Glacier Lake (Cuerrier, 1954), and Swan Lake on Clearwater River drainage (J. S. Nelson, personal communication).

Athabasca River system: Moab and Pyramid Lakes (Cuerrier, 1954), Rock Lake near Hinton (J. S. Nelson, personal communication), Graham and Legend Lakes (MacDonald, 1951), formerly present in Lesser Slave Lake.

Early reports of natural populations of lake trout in the Upper Columbia River, and from Vancouver Island, are almost certainly erroneous.

British Columbia: in the Skeena River system as far west as Morice Lake, the upper Stikine River System, the upper Taku River system, the upper Chilkat River system, and lakes in the Yukon, Liard and Peace River systems; in the Fraser River system from extreme headwater lakes to as far south as Shuswap Lake, but not recorded farther downstream except for two emaciated specimens taken by angling, one from Thomson River and the other from Coquihalla River (Carl *et al.*, 1959).

Admiralty Island (south of Juneau): Thayer Lake (SU 48538).

Headwaters of Alsek River system: Dezadeash Lake (specimen seen), Klukshu Lake (BC 57–242), Kathleen Lake (BC 57–247).

Headwaters of Copper River system: Paxson Lake (BC 58–229), Copper Lake (SU 48517).

Kenai Peninsula: Upper Trail Lake (BC 58–202), Skilak Lake (BC 58–223), Tustumena and Kenai Lakes (Dufresne, 1946).

Susitna River system: Lake Louise (BC 58–195).

Bristol Bay drainages: Ugashik Lakes (SU 48534-7), Naknek River system (Naknek, Brooks, Grosvenor and Coville Lakes (Greenbank, 1954) and Hammersley Lake (BC 62–382); Kuichak Bay drainages (Kukaklek, Iliamna and Clark Lakes (Dufresne, 1946); in headwater lakes of a number of drainages rising in the Kilbuck Mountains, including Nushagak River system (Titchik Lake, S. Y. Koo, personal communication); absent from the entire Wood River system (S. Y. Koo, personal communication); reported from Togiak River system (Nenovok Lake, D. Paddock, personal communication); reported from Goodnews River system (D. Paddock, personal communication); reported from Kanektok River system (Kagati Lake, D. Paddock, personal communication); Kuskokwim River system (Kisaralik Lake, BC 60–398; Aniak Lake, BC 60–397).

Yukon River system: reported to be present in Koyukuk River drainage but not in tributaries entering Yukon River below Koyukuk River mouth (S. Pennoyer, personal communication), Norutak Lake (Dufresne, 1946); Tanana River drainage (Wonder Lake, BC 63–1030; Tangle Lake, BC 58–231); Porcupine River drainage (Old John Lake, SU 48577); White River drainage (Kluane Lake, BC 57–250); most deep lakes in Yukon River headwaters from Lake Laberge south (Richtofen Lake, BC 58–293; Lake Laberge, specimen seen; Louise Lake, BC 60–22; several lakes in British Columbia (Carl *et al.*, 1959); Teslin Lake (Clemens *et al.*, 1945); Summit Lake at White Pass (Evermann and Goldsborough, 1907).

Seward Peninsula: In a popular account of Alaska's animals and fishes, Dufresne (1946) reports lake trout as occurring in Salmon Lake 40 miles north of Nome, but nowhere else in the vicinity. If this record is correct it locates the species much closer to Bering Strait than is indicated in Fig. 1. However, I have collected in Salmon Lake (June 23–24, 1960), and took both *Salvelinus alpinus* and *S. malma* (McPhail, 1961) but no *S. namaycush*. Dufresne's report therefore requires verification.

St. Lawrence Island (*Bering Sea*): lake trout are apparently absent, but 3 freshwater species have been taken, *Thymallus signifer* (BC 62–314), *Dallia pectoralis* (BC 60–382), and *Cottus cognatus* (BC 60–383).

Kobuk River headwaters: Lake Car-loog-ah-look-tah (= Walker Lake) (Townsend, 1887). About 400 miles east-northeast of Bering Strait.

North slope of Brooks Range: Colville River system (Tolugak Lake, Chandler Lake, Colville River at Umiat); lake near headwaters of Kuyula River; Sadlerochit River system (Schrader Lake); Hulahula River system (museum numbers and references in Walters, 1955).

Mackenzie River system: in waters of the delta at Kittigasuit (ROM 10258) and in the middle channel east of Aklavik (ROM 18044); in headwaters of the Peel River in the Wernecke Mountains (Hart Lake (BC 61–457), Fairchild Lake (BC 60–347)); widely distributed in suitable waters throughout the drainage.

Horton River system: lake at head of Coal Creek (Anderson, 1913).

Lakes at Bernard Harbour (Walters, 1953).

Coronation Gulf drainages: "in the mouths of some of the large rivers near Coronation Gulf" (Walters, 1953); delta of Coppermine River (stomach containing the marine capelin, *Mallotus villosus*) (Ellis, 1962); lakes on Coppermine River system (BC and ROM collections).

Banks Islands: Raddi Lake; Castel Bay, "in sea . . . actually it was no more than brackish" (Manning, 1953).

Victoria Island: lake on Wollaston Peninsula (Walters, 1953); lake adjacent to Cambridge Bay (ROM 13200).

Bathurst Inlet drainage: mount of Burnside River (water brackish, marine species nearby (Walters, 1953), also ROM 15101); Kathawachaga Lake (BC 60–82).

King William Island: occurs in considerable quantities in waters of King William Island, where it is the object of a rather important eskimo fishery during summer (Pfaff, 1937).

Back River: several lakes (BC and ROM collections).

Boothia Peninsula: river draining Netsilik Lake south of Spence Bay (Ellis, 1962).

Baffin Island: report of probable lake trout from lake near Bernier Bay (Ellis, 1962); fish from Hantzsch River 3 miles above mouth "almost certainly a lake trout", not kept (Manning, 1943).

Melville Peninsula: Hall Lake and larger lakes of Crozier River contain large rapacious fish, likely to be either lake trout or pike (Ellis, 1962); somewhere west of Repulse Bay (Manning, 1943).

West side Hudson Bay: many records from drainages entering west side (BC and ROM collections); specimen in American Museum of Natural History caught 5 miles offshore in Hudson Bay (Walters, 1953).

Quebec and Labrador: widely distributed in mainland drainages entering James Bay, Hudson Bay, Hudson Strait, Ungava Bay, Atlantic Ocean and Gulf of St.Lawrence (Harper, 1961); reported from two Labrador localities "in the sea" (Weed, 1934).

Salinity Preference: an Orientation Mechanism in Salmon Migration[1,2]

By John E. McInerney[3]

Institute of Fisheries, Dept. of Zoology
University of British Columbia, Vancouver, B.C.

ABSTRACT

An examination of the modal salinity preferences of five Pacific salmon species showed the following pattern of temporal changes. The sequence began with a preference for fresh water, then changed gradually, in the direction of increasing seawater concentration. The terminal pattern indicated a preference for water of open ocean concentration. This temporal progression of salinity preference changes was shown to parallel closely the salinity gradients typical of river outflows through which young salmon pass on their way to the ocean. On the basis of this evidence the following orientation mechanism was proposed: that juvenile Pacific salmon are able to use estuarial salinity gradients as one of the directive cues in their seaward migration.

INTRODUCTION

Contributions towards an understanding of the orientation mechanisms used by migrating salmon have been made in recent years by Wisby and Hasler (1954), Collins (1952), Hasler (1954, 1956), Johnson and Groot (1963) and the entire problem has been reviewed by Hasler (1960). The present work provides additional information on this subject. In particular, evidence will be described which suggests that juvenile salmon are able to use the salinity gradients characteristic of river outflows as an orientation guide during their seaward movements.

In assessing the possible orientation value of salinity gradients, the following three criteria were used as a study guide. First, it was considered necessary to show that naturally occurring salinity gradients are orderly enough to provide a reliable migration guide. A predictable series of salinity changes along the migration route would be necessary. Second, salmon should be shown to have the sensory and central nervous organization necessary for co-ordinating their movements in relation to salinity. Third, the salmon's response to salinity (preference or avoidance) should be shown to undergo an orderly sequence of temporal changes which parallels spatial changes in salinity along the migration route. The third criterion is the most subtle but the one providing the strongest circumstantial evidence of an orientation mechanism. Previously published evidence on the structure of estuarial gradients will be reviewed which satisfies the first criterion. Original evidence will be presented satisfying the second and third criteria.

[1]Received for publication July 3, 1963.

[2]Based on a thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy at the Department of Zoology, University of British Columbia.

[3]Present address: Zoological Laboratory, Dalhousie University, Halifax, Nova Scotia.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

MATERIALS AND METHODS

Experimental Animals

The five species of salmon endemic to Canada's west coast were studied; *Oncorhynchus keta* (chum), *O. gorbuscha* (pink), *O. tshawytscha* (spring), *O. nerka* (sockeye), and *O. kisutch* (coho). In nature the eggs of all five species hatch during the late winter and spring followed, after a variable period, by emergence from the gravel. Chum and pink salmon fry migrate to sea soon after emergence. By contrast coho fry spend one and sometimes two years in streams, and sockeye fry the same period in lakes, prior to seaward migration. Spring salmon may remain in fresh water for a variable period up to 15 months (Carl *et al.*, 1959).

All the animals used in this study were obtained from rivers which share as their common estuary the Strait of Georgia (a body of water separating Vancouver Island from mainland North America). Unless otherwise specified they were maintained in running fresh water in the University of British Columbia Aquarium. According to their food preferences they were fed one or more of the following preparations 2–3 times daily: Clark's trout food (pellets), frozen adult brine shrimp (*Artemia salina*), and/or a wet food mixture consisting of beef liver 65%, raw or cooked fish 21%, Pablum 8%, brewers yeast 6% plus 1 tsp iodized table salt per 300-g mixture. Prior to the normal period of seaward migration the experimental animals' growth approximated that of wild fish but after this point their growth progressively lagged behind wild fish. Seasonal changes in water temperature (4–15°C) and photoperiod (7–17 hr daylight) in the aquarium approximated those occurring naturally at this latitude. For experimental work only vigorous and otherwise apparently healthy animals were used.

Apparatus and Test Procedure

The original evidence to be presented has been obtained from the salinity preference test, a procedure which permits young salmon to choose between fresh water and a particular concentration of sea water in the range of 0–18‰ Cl. The method has been modified after Baggerman (1957) and Houston (1957). In the present work an array of 20 salinity preference test tanks were arranged side by side in a running water bath. One of the test tanks is pictured in Fig. 1–A. An incomplete partition divides the tank into 2 compartments each containing an airstone and bottom center inlet. To begin the test, the inlets in each compartment were first stoppered with rubber plugs, one solid and the other pierced by $\frac{1}{4}$-inch diameter hole leaving the latter compartment continuous with the surrounding water bath (Fig. 1–B). Next the test seawater solution was poured into the sealed compartment to the level of the partition (Fig. 1–C). Then the water bath was filled with fresh water so that the unsealed compartment was flooded to within approximately $\frac{1}{2}$–1 inch from the top of the partition (Fig. 1–D). At this point 8 fish were placed in the latter compartment, the air flow was started in both compartments and the apparatus was allowed to stand undisturbed for 3 hr (10 AM to 1 PM). This gave the fish an opportunity to adjust to their new environment and permitted the water in the test compartments to reach a uniform temperature equal to that of the running water bath (Fig. 1–E).

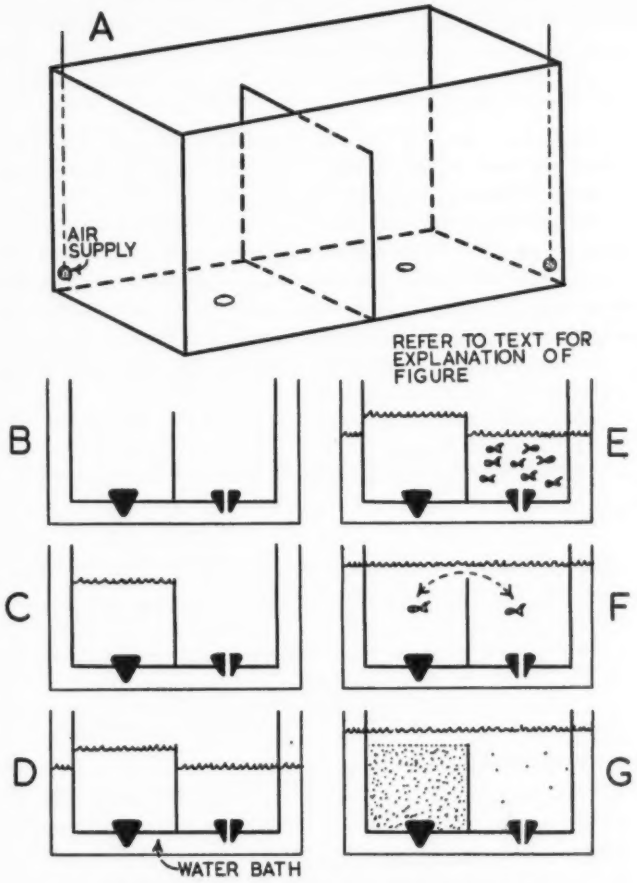


FIG. 1. Salinity preference tank and test procedure.

After 3 hr the air supply was turned off and the level of the surrounding water bath was again raised very slowly (10–15 min) so that a freshwater "bridge" was formed across the partition allowing the fish freedom of movement between the two compartments (Fig. 1–F). The depth of the bridge was adjusted to suit the size of fish. By making the bridge with fresh water, a relatively stable stratification was obtained with the less dense water on top. This is shown diagrammatically in Fig. 1–G. It is important to recognize that all tests were identical except for the concentration of sea water in the sealed compartment. Mounted above each tank was an observation mirror, two lights (G. E. Lumiline) and two reflectors, the latter functioning to prevent an image of the light bulb being reflected back from the water surface to the observer. The intensity of illumination was maintained at 1.5 ± 0.1 ft-c measured at the water surface directly over the partition and the temperature of the running water bath was equal

±0.2°C to that of the aquarium holding tanks in which the fish were normally kept. The entire apparatus was surrounded with black walls and curtains except for an eye-level slit through which observations were made from a darkened background.

Natural sea water varying seasonally between 12 and 15‰ Cl was used, which was obtained from Burrard Inlet. Dilutions were prepared with dechlorinated tap-water. More concentrated sea water was made by adding appropriate amounts of kiln-dried half-ground salt to natural sea water up to a combined total of 18‰ Cl. The salt thus added never accounted for more than one-third of the total chlorinity. Salinity determinations were made using the modified Mohr titration to an accuracy of ±0.2‰ Cl. Information in addition to that obtained by Houston (1956) on the stability of the test gradients is shown in Fig. 2. A comparison of mixing in tanks (a) without fish, (b) with small

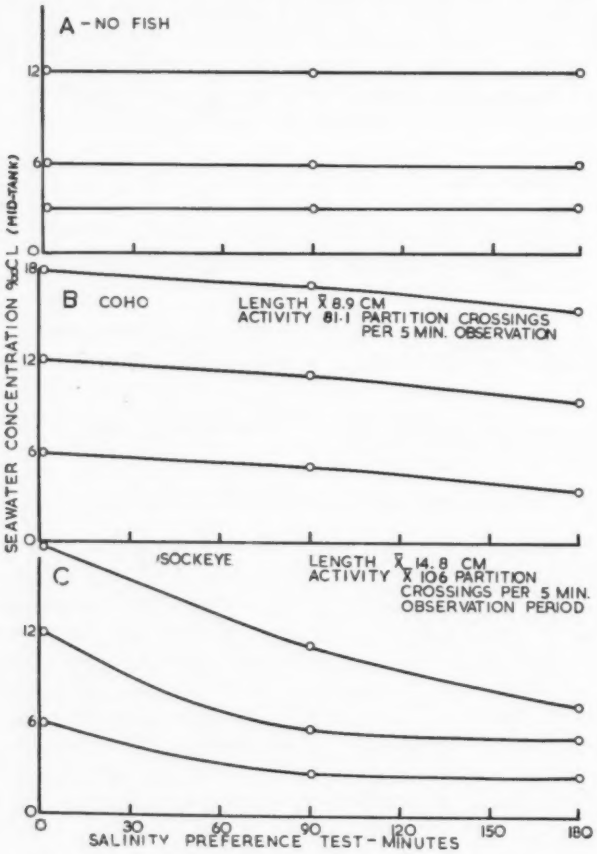


FIG. 2. Decline of salinity preference test gradients with time.

relatively inactive fish, and (c) with large and relatively active fish provides an indication of the variability in gradient breakdown. The results for the small and relatively inactive fish (b) represent the most typical condition in the present study. The seawater concentrations given in the results refer to the concentration at the beginning of each test.

Observations were made by recording the number of fish in each of the two compartments for a period of $2\frac{1}{2}$ hr according to the following schedule: once every 2 min for 20 min, followed by a 10–min pause, with the 20–10 cycle repeated five times. Fifteen to twenty replications of the above procedure for each seawater concentration were found to give consistent results. Generally a series of five seawater concentrations (0, 3, 6, 12, 18‰ Cl) was tested simultaneously. Four days were required for such a series, performing 20 tests per day, the maximum possible, with a total of 16 replications for each concentration. The distribution of test seawater concentrations in the 20-tank apparatus was arranged in a statistically random fashion, and the observations were taken without immediate knowledge as to which compartments contained particular seawater concentrations. A total of 6400 distribution observations was obtained for each concentration (8 fish per observation × 50 observations per fish per replication × 16 replications).

Past workers have used a variety of statistical tests of significance in evaluating these results (Baggerman 1957, 1960; Houston 1956, 1957). The use of such tests is of doubtful validity, however, for the following reasons. The probability statement derived from any test of significance is in part a function of the sample size. Thus, when a small percentage difference between 2 variables exists a large sample will produce a statistically significant difference and a small sample a non-significant difference. Salinity preference test results typically show differences of less that 30% and the sample size is therefore an important consideration. Statistically the sample size is equal to the total number of *independent* observations. On two accounts the degree of independence, and as a result the sample size, are difficult to determine in the case of salinity preference observations. First, the eight fish used in each test do not behave as independent units but frequently show a strong schooling behaviour. To complicate matters even further the intensity of schooling shows a very marked seasonal fluctuation making any attempt to estimate the degree of dependence extremely difficult. The second source of dependence is temporal in origin. Because the salinity preference observations are taken in fairly rapid sequence, any one observation is to a greater or lesser extent dependent on the preceding and successive observations. Because the salmon's general activity also shows very marked seasonal variations the degree of dependence is again difficult to evaluate. The net effect of these considerations is to make the "effective" sample size so uncertain a quantity as to be meaningless. One might plausibly argue that instead of the 6400 observations mentioned above there were really closer to 16 independent observations (the number of test replications). The use of tests of significance under such circumstances (that is where the sample size cannot be objectively determined) is without value. Accordingly, in the present work the results have

been evaluated in a different way. By simultaneously comparing the response to a selection of seawater concentrations approaching the salmon's natural salinity range, evaluations of biological significance have been based on an interpretation of the *pattern* of response to the various concentrations.

In the results, all the distribution observations have been converted to per cent differences in distribution in the seawater (sealed) compartments. The response to 0‰ Cl (fresh water) is used as the baseline. A negative value indicates a negative preference (avoidance) and a positive value a positive preference relative to fresh water. Any per cent figure may be reconverted to absolute values according to the following method. For example, in Fig. 5–C a response of +20% was shown to 3‰ Cl sea water. Back calculating, 1280 (+20% × 8 fish per observation × 50 observations per fish per replication × 16 replications = 1280) more fish were observed in the 3‰ Cl than in 0‰ Cl sea water (fresh water). The terms 8 and 50 are constants for all the data in this study. The per cent differences in distribution and number of replications are given in the appropriate section of results.

The main premise governing the experimental design adopted in this study was that the salmon should frequently choose between the offered alternatives. This seems basic to the objective measurement of any preference. This was accomplished by confining these active fish species to relatively small tanks so that the choice salinities were frequently encountered. Additional effects of this design were distribution observations showing small overall differences and considerable response variability in individual experiments. The combined results, however, showed a good degree of consistency and replicability as will be shown in the Results. It is on these combined results that the interpretations of this study are based.

RESULTS

Temporal Changes in Salinity Preference

Chum salmon

The temporal changes in salinity preference which chum salmon fry undergo are illustrated in Fig. 3. The most important feature of these observations is the orderly sequence of salinity preference changes. Beginning with a modal preference for fresh water (0‰ Cl) in May, the sequence changes through 3‰ Cl in June, 6‰ Cl in July, approximately 8‰ Cl in August and finally 10‰ Cl in October. This feature is emphasized in Fig. 3-F. Several other points also merit comment. First, the overall shape of the curves suggests a rather wide latitude in preference. Second, an indication of the consistency of the response pattern may be gained from Fig. 3–A. Even though each seawater concentration was tested separately the composite response pattern shows a high degree of regularity. Third, not only does the preferred concentration change in an orderly sequence but the intensity of response does also. From a 14.3% response to 3‰ Cl (Fig. 3–B) the response intensity increases to 25–30% for the subsequent preferred concentrations. Fourth, the temporal sequence of salinity preference changes

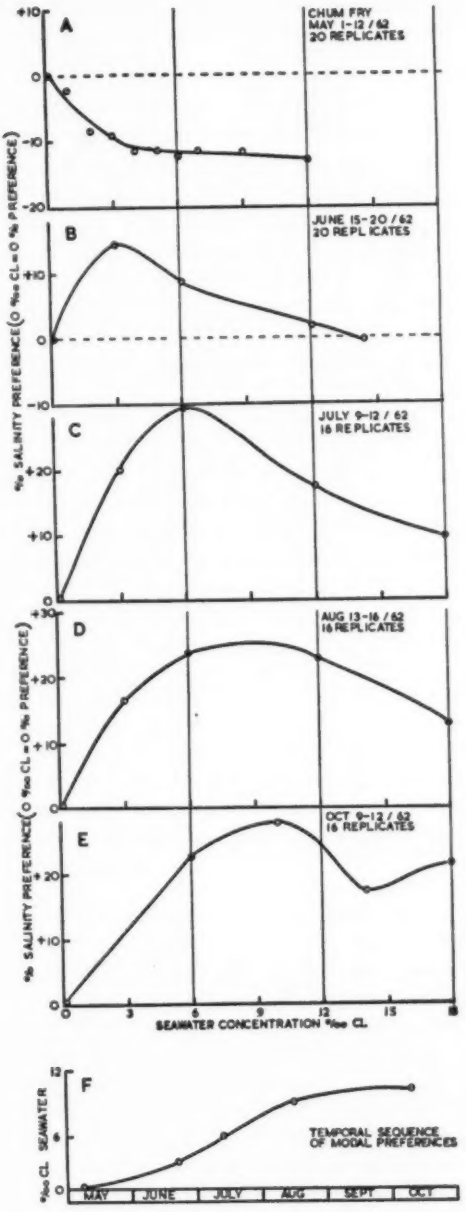


FIG. 3. Temporal sequence of salinity preference changes, chum salmon.

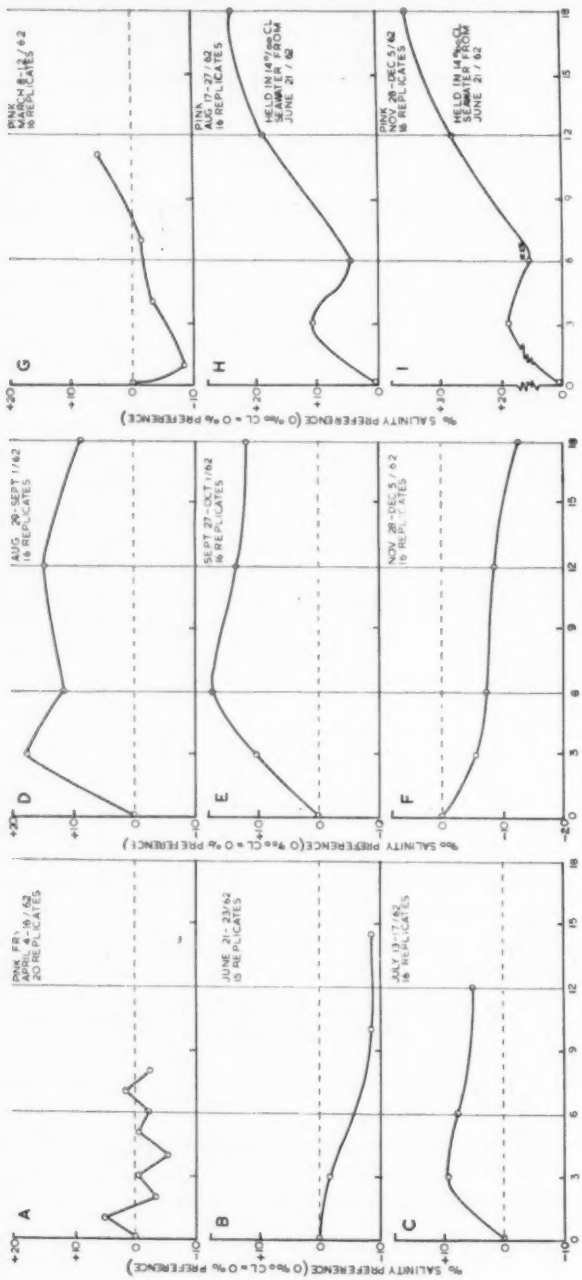


FIG. 4. Temporal sequence of salinity preference changes, pink salmon.

appears to be basically independent of any prolonged exposure to sea water since the test animals in these experiments were confined to fresh water except during the salinity preference tests.

PINK SALMON

Comparable data for pink salmon are given in Fig. 4. These observations are for fish maintained in fresh water and cover almost a full calendar year (Fig. 4-A to G, inclusive). The April response suggests that the fish do not orient with respect to sea water at this early stage of development. From June through September the responses are similar to those for chum showing an orderly sequence of changes in modal preference and response intensity. The November response shows a new feature, a complete reversal to the June condition when fresh water was preferred. Pinks tested as yearlings in March demonstrate the cyclical nature of the salinity preference sequence by redeveloping a preference for concentrated sea water (11.0‰ Cl).

Graphs H and I in Fig. 4 show the responses of pink fry maintained in 14‰ Cl sea water from June 21, 1962, instead of fresh water. In contrast to the freshwater fish which prefer 3‰ Cl in August the seawater fish at this time prefer 18‰ Cl, a concentration equivalent to open ocean sea water. Further, the seawater fish when tested in November still preferred 18‰ Cl and even increased their response intensity from 23.7 to 35.1% unlike the freshwater fish whose pattern had by November reverted to a freshwater preference.

In summary, pinks appear to show basically the same temporal sequence of salinity preference changes as chum, with the following additional features. When confined to fresh water they undergo an incomplete (<0–18‰ Cl) sequence of salinity preference changes eventually reverting to a freshwater preference. Those held in salt water undergo a complete sequence of changes (0–18‰ Cl) and do not show a reversion to a freshwater preference. Prolonged seawater exposure seems to have three effects; first, it accelerates the development of the preference sequence, second, it extends the sequence to include water of open ocean concentration, and third it blocks a reversion to a freshwater preference.

COHO SALMON

A more detailed series of data on the early stages of the salinity preference sequence are given in Fig. 5. These observations are for coho, a species which commonly migrates to sea as a smolt after spending 1 year in fresh water. In agreement with this pattern of migratory behaviour, their salinity preference never goes beyond 3‰ Cl during their first year. This fact is also consistent with the observation that coho are often found in the inner estuarine region as underyearlings. Graphs A to C of Fig. 5, showing a change in preference from 0 to 3‰ Cl, provides evidence that the salinity preference sequence is a smooth series of changes rather than a number of discontinuous steps. A final proof of this point would require a much more detailed analysis than was possible in this study. Figure 5-D shows a series of observations made during July and August of 1961 whereas all the other data of Fig. 5 were obtained during 1962. The similarity of the response pattern for the 2 years demonstrates the replicabi-

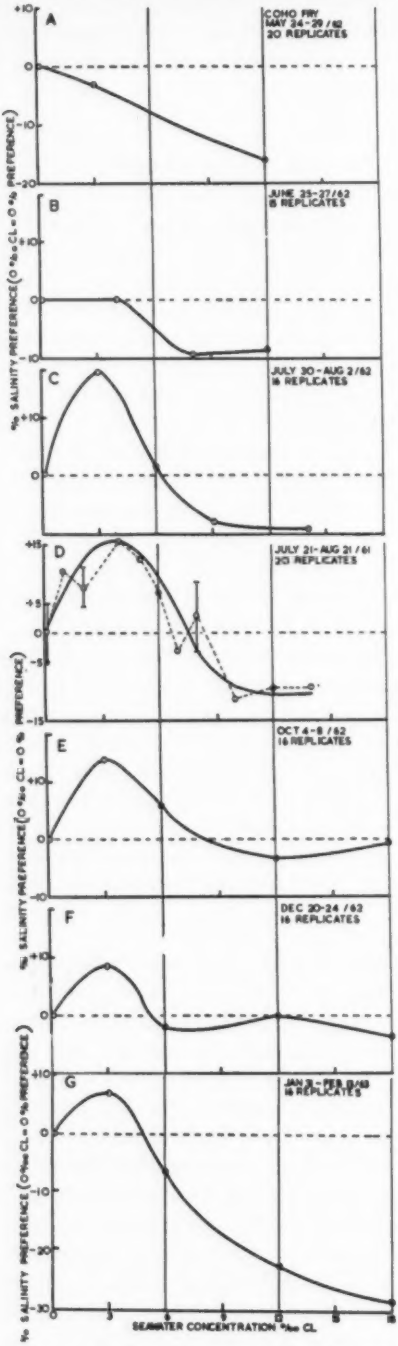


FIG. 5. Temporal sequence of salinity preference changes, coho salmon.

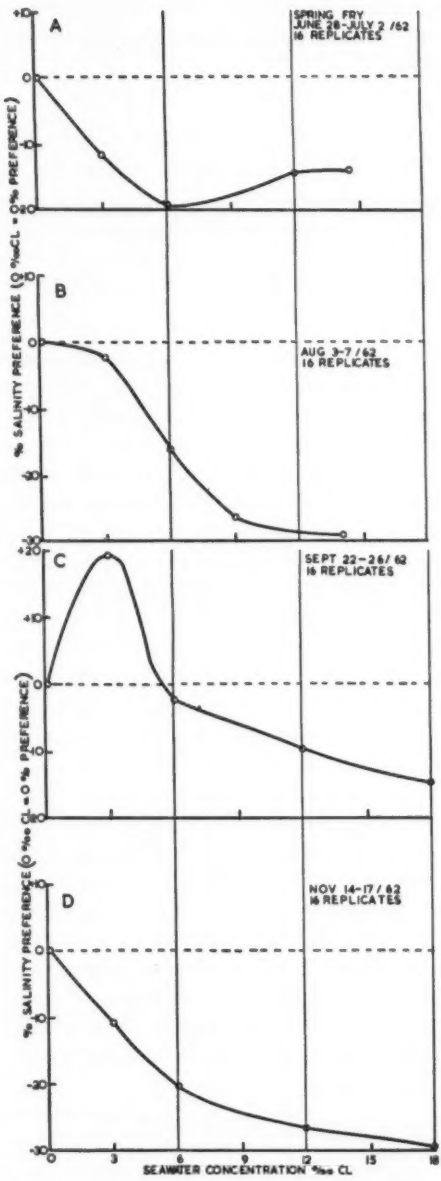


FIG. 6. Temporal sequence of salinity preference changes, spring salmon.

lity of the salinity preference response for a single species obtained from different sources, and for successive year-classes. One further point is the absence of any sign of a regression to a freshwater preference as was the case with pink salmon confined to fresh water.

Spring salmon

Figure 6 illustrates the sequence of salinity preference changes of spring fry retained in fresh water. Though the data are limited the sequence most closely resembles that of pink, particularly since the pattern reverts to a freshwater preference by November. This preference sequence is consistent with this species normal migratory behaviour (these animals were obtained from the Samish Hatchery in Washington State, a stock which migrates to sea as underyearlings).

Sockeye salmon

The salinity preference sequence for sockeye underyearlings (fry) and yearlings (smolts) is somewhat puzzling. During May, sockeye fry show two distinct preference peaks (Fig. 7). The peak occurring at approximately 3‰ Cl is similar to that shown by coho fry at about the same time. The second peak at about 14‰ Cl is apparently unique to sockeye. The reality of the two peaks is confirmed by the June curve which shows substantially the same pattern. From September to December the modal preference remains at approximately 3‰ Cl though some traces of the anomalous second peak are still evident. The January pattern clearly shows a single preference peak and this is followed by an orderly progression of preference changes which is terminated by a preference for 18‰ Cl in August. When tested in October no pattern is evident suggesting a regression similar to those shown by pink and spring retained in fresh water.

Several points are important. First, sockeye generally migrate to sea as yearlings and the results are broadly consistent with this fact since the preference sequence does not go beyond 3‰ Cl during their first year. According to Clemens and Wilby (1961) some sockeye migrate as fry. The anomalous 14–15‰ Cl preference peaks may (in some way not as yet clear) be connected with this fact. Second, sockeye, unlike chum, pink, and spring, seem to undergo a complete sequence of salinity preference changes when confined to fresh water. Third, the preference pattern shown in Fig.7–I, although superficially similar to the double peak patterns discussed above, must be evaluated quite differently since it is the terminal pattern of the preference sequence. At this time the fish would already have passed mid-estuary and would be entering oceanic waters. The double peak may result from a decreasing preference for salinities through which the migrants have most recently passed making it even more unlikely that they would re-enter the estuary.

Effects of Repeated Testing

The acceptance of the forgoing temporal sequence of salinity preferences as valid is based on a number of assumptions. First, it is assumed that the changes measured in the laboratory approximate those occurring in nature. The good agreement, between the salinity preference observations and the published

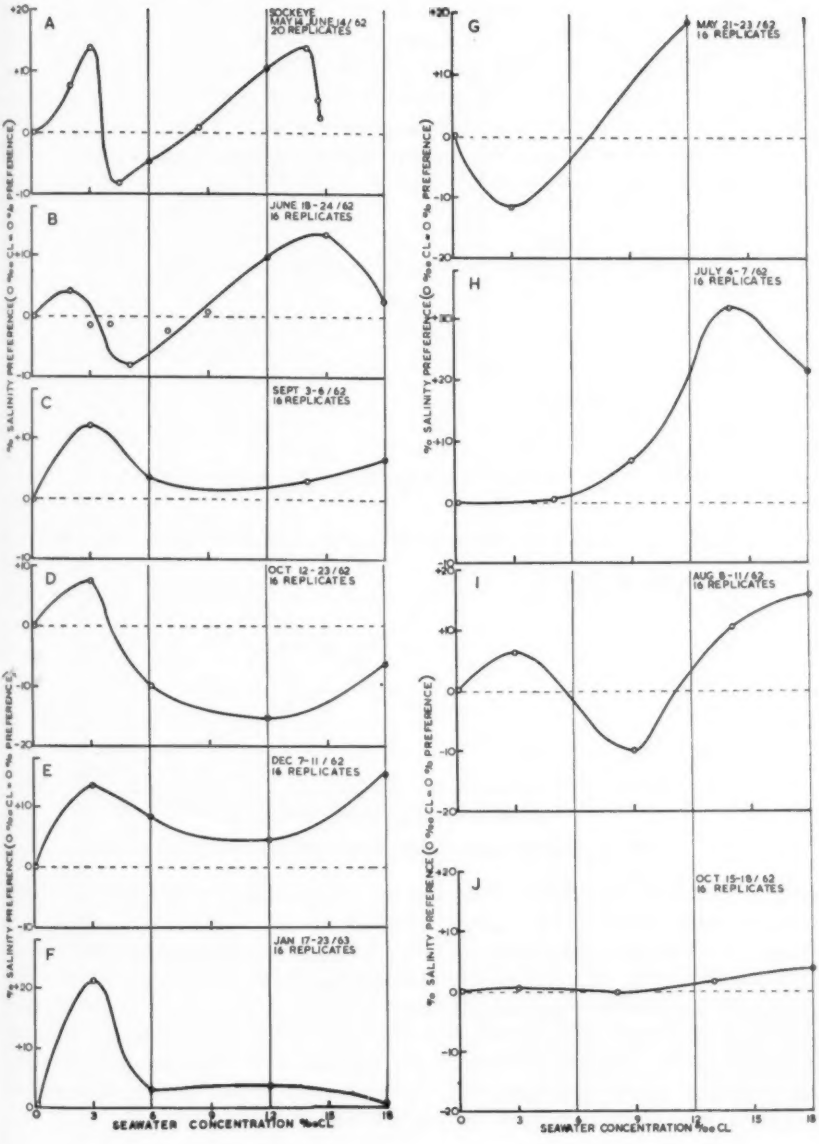


FIG. 7. Temporal sequence of salinity preference changes, sockeye salmon.

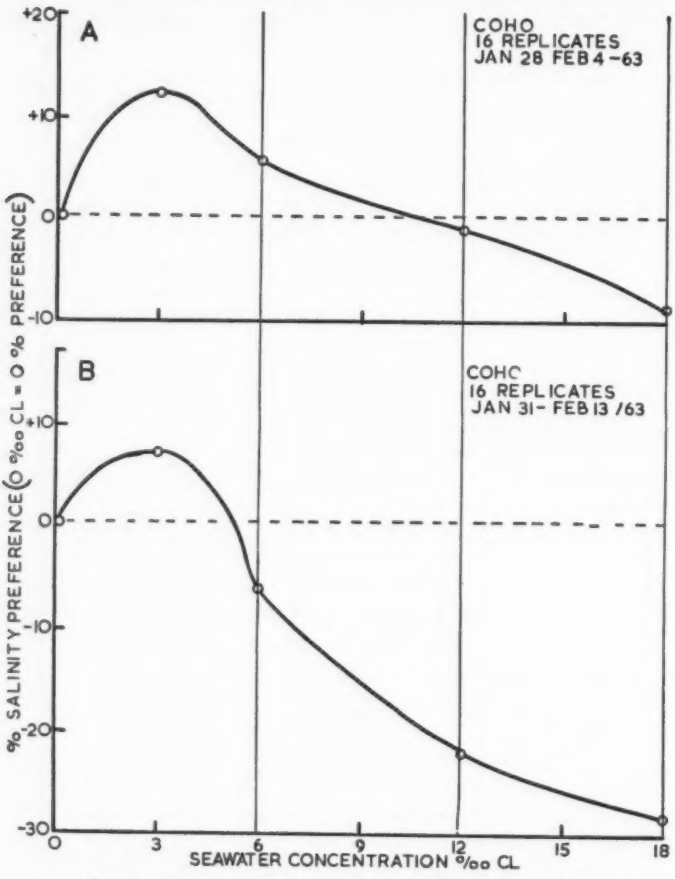


FIG. 8. Effects of repeated testing on salinity preference.

information on the migratory habits of the various species cited above, makes this a broadly plausible assumption. Second, that the sequence of preference changes is not merely the result of repeated testing is demonstrated by the results presented in Fig. 8. Curve B of Fig. 8 shows the preference pattern of coho fry which had been tested on seven previous occasions, and curve A is for animals which had never before been tested but which had otherwise been kept under the same laboratory conditions. Despite the differences in response intensity the clearly similar modal preferences (3‰ Cl) demonstrates that the development of the preferences sequence is certainly not a laboratory artifact.

EFFECTS OF SEAWATER EXPOSURE

The forgoing results are interesting in another respect. Group B (Fig. 8) by virtue of repeated testing had been exposed to sea water on several occasions.

Group A although never before exposed to sea water showed the same modal preference thereby demonstrating that prior contact with sea water is unnecessary for the development of the initial part of the salinity preference sequence. The effects of sea water on salinity preference were further examined by exposing underyearling coho to several seawater concentrations for varying periods prior to testing. In the first experiment the fish were simply put into the salt-water compartment of the salinity preference tanks for the initial 3-hr adjustment period instead of the usual freshwater compartment. Comparing the preference pattern of the seawater fish (Fig. 9–A) with that of the controls (Fig. 5–F), the

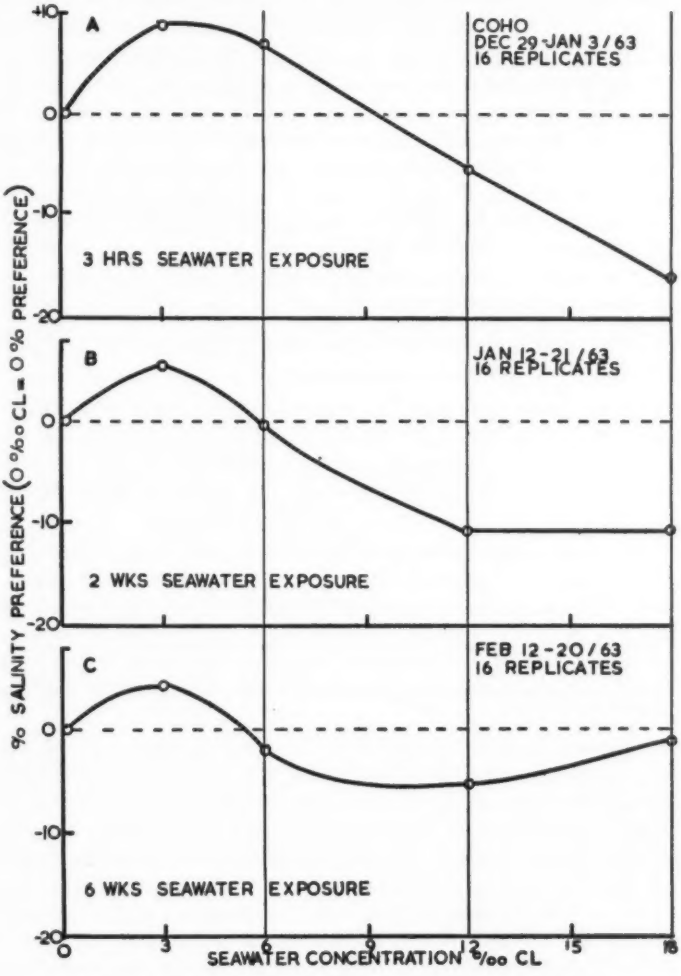


FIG. 9. Effects of seawater exposure on salinity preference.

same modal preference (3‰ Cl) is evident. In the second and third experiments, coho fry were kept in 12‰ Cl sea water for periods of 10 days (Fig. 9–B) and 6 weeks (Fig. 9–C), respectively. In both cases the modal preference remained unchanged at 3‰ Cl. Summarizing, it would appear that the initial part of the preference sequence develops unaffected by seawater exposure (the sequence is initiated independently of any seawater contact and even prolonged exposure will not subsequently alter this development).

Combining these results with those presented earlier for pink fry (where it was shown that the latter part of the salinity preference sequence only developed in those fish which had been exposed to 12–15‰ Cl sea water for 3 months) the following tentative generalizations emerge. The initial part of the preference sequence (0 to approximately 6–9‰ Cl) normally develops independently of any exposure to sea water and is not altered by continuous exposure up to 6 weeks. Development of the latter part of the sequence depends on a period of seawater exposure. In the present case, 3 months exposure to 12–15‰ Cl was effective, however it is probably safe to speculate that shorter periods of exposure to concentrations of the order of 3–6‰ Cl would be adequate. These conditions the migrants would naturally encounter during the early part of their seaward movements. It is apparent from the forgoing that a completely satisfactory description of the salinity preference sequence and its normal timing would require facilities where the animals could be held at their preferred seawater concentration instead of being confined to fresh water or to some single seawater concentration.

DISCUSSION

Three criteria were proposed as a study guide in the Introduction. First, it was considered necessary to show that salinity gradients are sufficiently constant and orderly features of river mouths to provide a reliable migration guide. The work of the Pacific Oceanographic Group of the Fisheries Research Board of Canada on estuarine salinity structure is especially useful. Not only does it constitute the most comprehensive information available but it also deals with the estuaries typically frequented by the species of salmon used in this study. In Fig. 10–A the surface salinities of a northern river outflow are shown diagrammatically. A regular seaward progression of increasing salinities is plainly evident. Examination of the elevation diagram (Fig. 10–B) shows vertical as well as horizontal gradients. Representative vertical sections are shown in greater detail in Fig. 10–C.

Some understanding of the stability of stratification and the dynamics of the system may be gained when it is realized that fresh water flowing into the ocean overruns the adjacent coastal sea water forming a surface layer of brackish water. This "...surface water remains on the surface and when removed from the influence of coastal streams, the salinity of the sea surface increases in the direction of flow because of progressive dilution with underlying sea water and removal of fresh water by evaporation. In this process ...deep water is transferred upwards but no fresh water is transferred downwards. Freshwater influence is finally lost by infinite dilution with sea water when the upper zone becomes indistinguishable from the lower zone" (Tully, 1952).

A number of factors may influence estuarine salinity structure including the geography of the surrounding land, tidal fluctuations and current, wind, and changes in river discharge. When, for example, the seaward surface flow is opposed by strong winds, the surface layer increases in depth which in turn has the effect of displacing the series of isohalines shown in Fig. 10–A in a seaward direction (Tully, 1952; Tabata and Pickard, 1957). Additional examples of estuarine salinity structure are given by Tully (1949, 1952) for Alberni Inlet and Chatham Sound; by Tabata and Pickard (1957) for Bute Inlet; by Tully and Dodimead (1957), and Waldichuck (1952, 1957), for Georgia Strait; and by Pickard (1961) in a review of British Columbia mainland inlets. In summary, estuarial salinity gradients satisfy the requirements of the first criterion as orderly,

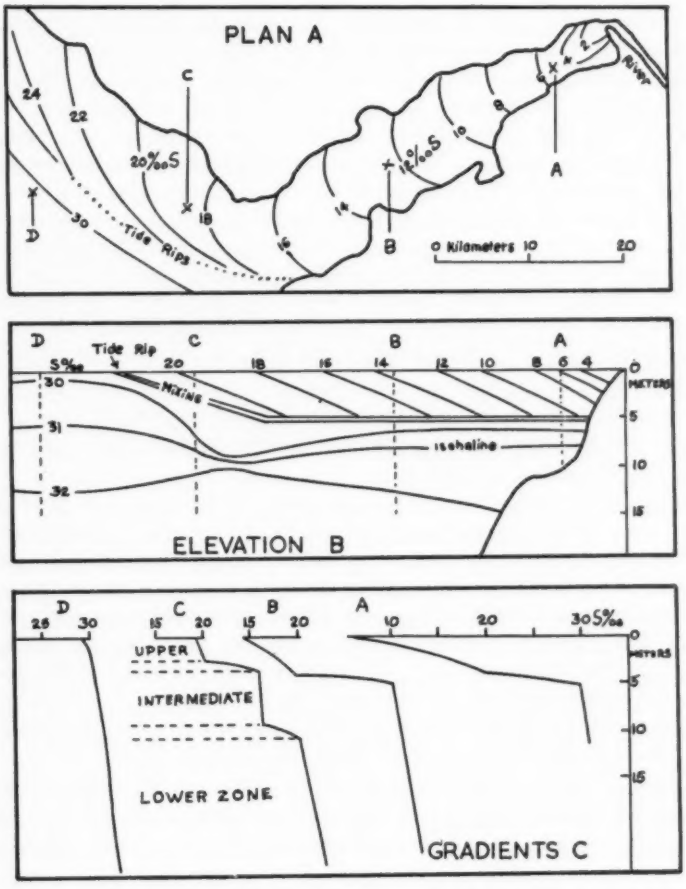


FIG. 10. Salinity gradient structure in the vicinity of a northern river outflow. (Modified after Tully, 1952.)

persistent, and predictable features of river outflows. The horizontal gradients are of special importance since salmon migrations are in the main horizontal movements. The possibility of more subtle vertical movements in relation to vertical salinity gradients is not discounted though they will not be considered here. Likewise, the possibility that salmon can use the more subtle coastal gradients (Tully, 1952; Lane, 1962) is a problem open to future investigation. Measurements approaching the order of magnitude of these offshore gradients were not attempted in the present study.

Attention will now be turned to the second criterion. This states that the animal should be shown to possess the sensory and central nervous organization necessary for co-ordinating its movements in relation to salinity. The entire body of salinity preference data presented in the Results argues strongly that juvenile salmon are capable of positioning themselves in salinity gradients. The only difficulty is that the experimental salinity gradients are considerably steeper than those occurring naturally. This is probably not a serious problem for the following reason. By testing the responses to each seawater concentration separately it was demonstrated that juvenile salmon are capable of showing a specific response to a particular seawater concentration *even when removed from the natural context of a continuous gradient.* This ability to show a specific response to a particular stimulus value without reference to two or more values of the stimulus (in other words without a scale of reference) is usually termed absolute discrimination as opposed to differential discrimination. By virtue of this absolute salinity discrimination, the difference in steepness of the experimental and natural gradients is probably not important and thus their behaviour in the relatively steep experimental gradients ought to be the same as in the shallower estuarine gradients. In summary, the behaviour of the fish in the salinity preference gradient tanks clearly indicates that juvenile salmon are able to detect and to position themselves with respect to differences in salinity thus satisfying the second criterion.

The third criterion requires that the response to the natural range of salinity be shown to undergo a sequence of temporal changes which parallels spatial changes in salinity along the migration route. Stated in a different way, the utility of salinity gradients and salinity preference as complementary parts of an orientation mechanism useful for migrations depends on a correspondence between the temporal sequence of preference changes and the spatial sequence of salinity changes along the migration route. A comparison of these two variables shows that juvenile salmon undergo a series of salinity preference changes which closely parallel the seaward progression of increasing salinities which they would encounter during their seaward movements through the estuarial region.

All three criteria having been satisfied the following hypothesis is proposed: that the salinity preference response of juvenile salmon reflects an ability to use estuarine salinity gradients as a means of orientation during their seaward migration.

The role played by the proposed orientation mechanism will now be considered in greater detail. The downstream migrant having reached the inner

estuarial region finds an environment very different from the river. The net transport of water although still seaward, is masked by the effects of complex tidal oscillations. Moreover, estuarial water is frequently turbid and the overall dimensions of the environment gradually increase so that the depth and horizontal dimensions are many times those of the river proper. In an otherwise difficult environment salinity gradients offer a potentially useful set of orientation cues.

Coho salmon as underyearlings remain in the rivers never progressing further than the upper estuarine region. Consistent with this behaviour their salinity preference never goes beyond 3‰ Cl (Fig. 11-A). I am indebted to Dr J. P. Tully for bringing my attention to the following facts. In Fig. 11 (band C) it is shown that as the tide rises a "salt wedge" intrudes into the river mouth forming a boundary layer between the fresh water and intruding sea water. Since the freshwater and seawater flows oppose each other a boundary zone is formed as a tide rip or convergence which moves back and forth in the river mouth according to the stage of the tidal cycle. Figure 11 shows further that the boundary layer actually forms a salinity barrier so that a 3‰ Cl salinity preference corresponds to the river side of the boundary layer (Tully and Dodimead, 1957). This close coincidence between the modal preference and salinity barrier suggests that the latter is perhaps the environmental factor which restricts coho fry distribution to the upper estuary.

Some knowledge concerning the distribution and movements of the other species in the estuarial region is available. Recent studies by Manzer (1956) and Manzer and Shepard (1962) indicate that the passage of juvenile salmon through estuaries is leisurely, covering a period of 3–5 months (April to August approximately in the case of pink and chum). Considering the rapid growth during this period it is not unreasonable to think of them as using the estuarial region as a nursery prior to moving into the open ocean. With this in mind the rather wide latitude in the most preferred seawater concentration, a feature of all the salinity preference data, gains some significance. Rather than covering a direct route between the river mouth and ocean, one might anticipate considerable wandering or to-and-fro movements within the estuary. As the migrants encounter water more or less saline than their modal preference they presumably make corrective movements which keep them within a rather broad area of preference, but with a gradual net movement in a seaward direction as their preference changes towards sea water of open ocean concentration.

When the size of seaward migrating pink salmon (up to 15 cm, Manzer and Shepard, 1962) is considered in relation to the steepness of the estuarine salinity gradients (approximately 0.0000035‰ salinity/cm calculated from Fig. 10-A), the method by which they correct their movement in the gradient poses some difficulty. A taxis form of orientation seems most unlikely, because of the shallow gradient. According to Fraenkel and Gunn's (1961) classification of orientation movements, the salinity preference mechanism would by elimination be classed as a kinesis. Two types of kinesis have been described. In the first, orthokinesis, locomotion is random in direction and the speed or frequency varies according to the intensity of stimulation. Woodlice (sowbugs) for example,

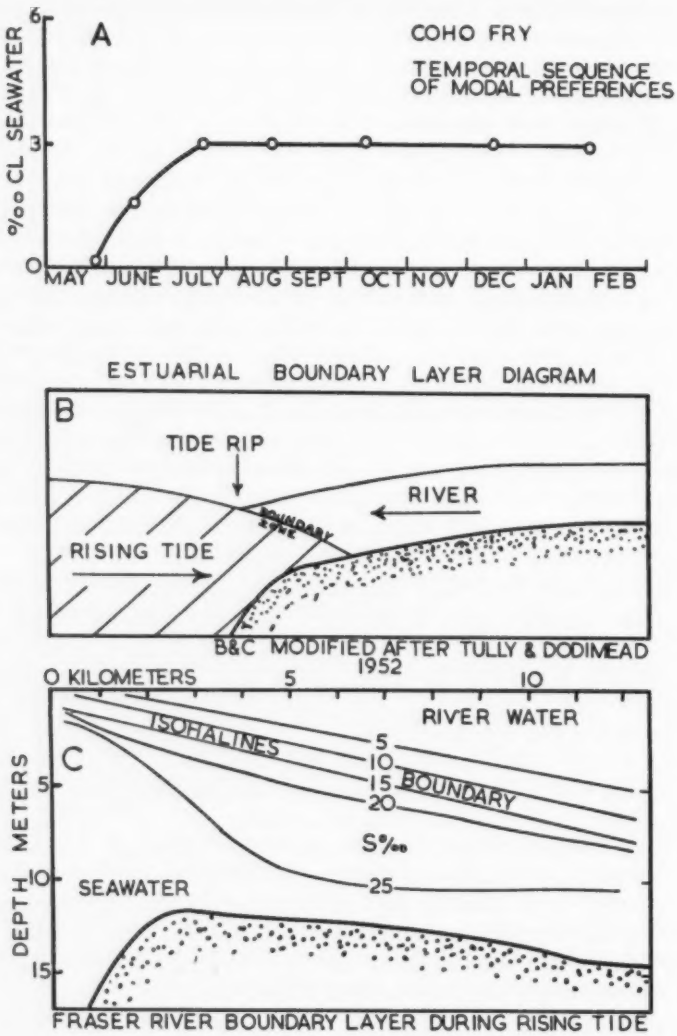


FIG. 11. Underyearling coho salinity preference pattern as related to the estuarine boundary layer. (B and C modified after Tully and Dodimead, 1952.)

find the humid areas essential to their survival by constantly moving (random direction) when they find themselves in an overly dry environment. Conversely they move relatively little when they discover their preferred humidity. Such a mechanism is obviously adaptive only when there is a good chance of finding the preferred region. This would be an unworkable mechanism in the present

case because the preferred salinity constitutes only a small percentage of the total environment (Pacific Ocean and contributing drainages). In the second type of kinesis, klinokinesis, the rate or frequency of turning is proportional to the intensity of stimulation and this, coupled with the phenomenon of sensory adaptation permits the animals to remain within a narrowly circumscribed region of preference. The "trial and error" behaviour of paramecia remaining within a drop of water more acid than that surrounding is a familiar example of klinokinesis (Fraenkel and Gunn, 1961). Sufficient evidence is not available to characterize the salinity preference mechanism as klinokinetic. In fact, absolute salinity discrimination might be incompatible with the sensory adaptation essential to klinokinetic orientation. All that can be concluded is that, within Fraenkel and Gunn's framework, salinity preference is probably a kinesis and of the two types described it resembles klinokinesis more closely than orthokinesis. It is, of course, also possible that other unrelated cues are used to make corrective movements within the salinity gradient and useful visual cues could be imagined. In this case salinity preference could be looked upon as the "fine adjustment" mechanism within a more generalized and less refined means of orientation. In either case the salinity preference orientation mechanism can only be referred to the Fraenkel and Gunn classification in certain features. An additional variable, not considered in their classification, is the temporal sequence of preference changes by virtue of which, each corrective movement is finally woven into an orderly pattern leading to the seaward displacement of the young salmon. A further modifying variable is schooling behaviour. Laboratory measurements show schooling intensity to be at the peak of its seasonal development during the time that the young salmon are moving through the estuary (McInerney, 1963). While a school of fish cannot be treated as a super-organism, individuals in the school no doubt gain certain advantages. It is even possible, though completely speculative, that a group might be large and orderly enough to permit aligning of the long axis of the school with the salinity gradient and thereby to achieve a taxis type of orientation.

In conclusion, the salinity preference orientation mechanism and its development is presented diagrammatically in Fig. 12. The initial part of the preference sequence (A) develops unaffected by seawater exposure. For the latter part of the sequence two routes of development are possible depending on seawater exposure. Those animals kept in fresh water (except for periodic preference testing) undergo a partial sequence of preference changes and then revert to a freshwater preference (Curve A–B). Those animals exposed to sea water (minimal exposure not established) during the initial part of the sequence undergo a complete series of salinity preference changes with the terminal modal preference for water of open ocean concentration (Curve A–C). Finally, the close correspondence between the sequence of salinity preference changes and the salinity gradients typical of estuaries, the essence of the arguments presented, is illustrated by the parallel curves in Fig. 12.

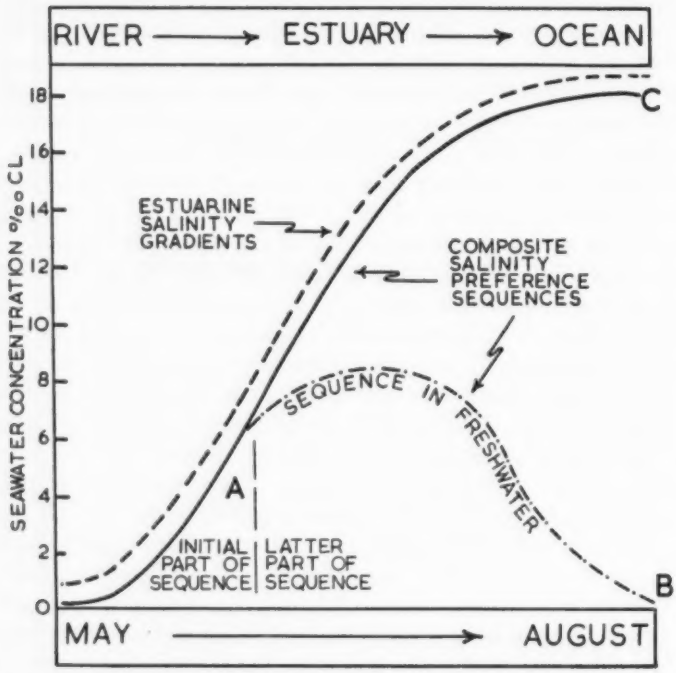


FIG. 12. Diagrammatic representation of the salinity preference orientation mechanism.

ACKNOWLEDGMENTS

I wish to thank especially Dr W. S. Hoar under whose direction this study was carried out. His inspiration and assistance are very much appreciated. I tender my thanks also to Drs J. P. Tully, P. A. Larkin, C. C. Lindsey, T. G. Northcote, R. N. Band, and J. F. Eisenberg all of whom criticized the manuscript in thesis form. The salmon used in the study were obtained with the generous cooperation of a number of agencies including the Department of Fisheries of Canada, the Fisheries Research Board of Canada, the Fish and Game Branch of the British Columbia Department of Recreation and Conservation, the Washington State Fisheries Department, and the International Pacific Salmon Fisheries Commission. Special thanks are due to Dr H. H. Harvey of the Salmon Commission for his generous assistance. Food for the salmon was kindly supplied by Mr J. Terpenning of the British Columbia Department of Recreation and Conservation and the J. R. Clark Company of Salt Lake City, Utah. The study was made possible through a National Research Council research grant to Dr W. S. Hoar and National Research Council and Fisheries Research Board Studentships held by the author, covering the period 1960 to 1963.

REFERENCES

BAGGERMAN, B. 1957. An experimental study of the timing of breeding and migration in the three-spined stickleback (*Gasterosteus aculeatus*, L.). *Arch. Neerl. Zool.*, **12**: 105–318.

1960. Salinity preference, thyroid activity, and the seaward migration of four species of Pacific salmon (*Oncorhynchus*). *J. Fish. Res. Bd. Canada*, **17**: 295–322.

CARL, G. C., W. A. CLEMENS AND C. C. LINDSEY. 1959. The fresh-water fishes of British Columbia. *British Columbia Prov. Mus., Handbook* No. 5 (third edition), 192 pp.

CLEMENS, W. A., AND G. V. WILBY. 1961. Fishes of the Pacific coast of Canada. *Bull. Fish. Res. Bd. Canada*, No. 68 (second edition), 443 pp.

COLLINS, G. B. 1952. Factors influencing the orientation of migrating anadromous fishes. *Bull. U.S. Bur. Fish., Bull.* No. **52**: 375–396.

FRAENKEL, G. S., AND D. L. GUNN. 1961. The orientation of animals. Dover Publications Inc., New York, 376 pp.

HASLER, A. D. 1954. Odour perception and orientation in fishes. *J. Fish. Res. Bd. Canada*, **11**: 107–129.

1956. Perception of pathways by fishes in migration. *Quart. Rev. Biol.*, **31**(3): 200–209.

1960. Homing orientation in migrating fishes. *Ergebn. Biol.*, **23**: 94–115.

HOUSTON, A. H. MS, 1956. An experimental study of the responses of young Pacific salmon to sharp sea water gradients. M. A. Thesis, Department of Zoology, University of British Columbia, Vancouver, B.C.

1957. Responses of juvenile chum, pink and coho salmon to sharp sea water gradients. *Canadian J. Zool.*, **35**: 371–383.

JOHNSON, W. E., AND C. GROOT. 1963. Observations on the migrations of young sockeye salmon (*Oncorhynchus nerka*) through a large complex lake system. *J. Fish. Res. Bd. Canada*, **20**: 919–938.

LANE, R. K. 1962. A review of the temperature and salinity structures in the approaches to Vancouver Island, British Columbia. *J. Fish. Res. Bd. Canada*, **19**: 45–91.

McINERNEY, J. E. MS, 1963. Salinity preference — an orientation mechanism in salmon migration. Ph.D. thesis, Department of Zoology, University of British Columbia, Vancouver, B.C.

MANZER, J. I. 1956. Distribution and movement of young Pacific salmon during early ocean residence. *Fish. Res. Bd. Canada, Prog. Rept. Pacific Coast Sta.*, No. 106, pp. 24–28.

MANZER, J. I., AND M. P. SHEPARD. 1962. Marine survival, distribution and migration of pink salmon off the British Columbia coast. H. R. MacMillan Lectures in Fisheries, Pink Salmon Symposium, 1960. Institute of Fisheries, University of British Columbia, pp. 113-122.

PICKARD, G. L. 1961. Oceanographic features of inlets in the British Columbia mainland coast. *J. Fish. Res. Bd. Canada*, **18**: 907–999.

TABATA, S., AND G. L. PICKARD. 1957. The physical oceanography of Bute Inlet, British Columbia. *J. Fish. Res. Bd. Canada*, **14**: 487–520.

TULLY, J. P. 1949. Oceanography and prediction of pulp mill pollution in Alberni Inlet. *Bull. Fish. Res. Bd. Canada*, No. 83, 169 pp.

1952. Notes on the behaviour of fresh water entering the sea. *Proceedings 7th Pacific Science Congress*, **3**: 1–22.

TULLY, J. P., AND A. J. DODIMEAD. 1957. Properties of the water in the Strait of Georgia, British Columbia, and influencing factors. *J. Fish. Res. Bd. Canada*, **14**: 241–319.

WALDICHUK, M. 1952. Oceanography of the Strait of Georgia. 1. Salinity Distribution. *Fish. Res. Bd. Canada, Prog. Rept. Pacific Coast Sta.*, No. 93, pp. 26–29.

1957. Physical oceanography of the Strait of Georgia. *J. Fish. Res. Bd. Canada*, **14**: 321–486.

WISBY, W. J., AND A. D. HASLER. 1954. Effect of olfactory occlusion on migrating silver salmon (*O. kisutch*). *J. Fish. Res. Bd. Canada*, **11**: 472–478.

Estimation of Sea Mortality Rates for the 1960 Brood-Year Pink Salmon of Hook Nose Creek, British Columbia[1,2]

By Robert R. Parker

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Seaward migrating pink salmon fry at Hook Nose Creek, British Columbia, were estimated to total 1,153,000 in 1961. Of these, 41.5% or 479,000, were marked by amputation of both ventral fins (BV). Following this marking 36,900 fingerling were captured in the marine environment and marked by removal of the adipose and right ventral fins (ARV). During the 1962 fishing season 1,160,645 adult pinks were examined and 7050 BV and 184 ARV marks recognized. For the Hook Nose Creek stock, survival at sea from natural causes is shown to approximate 22% and the rate of exploitation was 95%. This stock is shown to be more exposed to fishing than the Bella Coola stock, for which a rate of exploitation of 69–80% is estimated. Rate of exploitation for Dean Channel stocks is even lower. These differences are explained as due to times of entry and rates of travel through the fishery. The two-stage marking experiment failed to estimate the natural mortality rate of juvenile pinks during the initial 5 weeks of sea life because of this dissimilarity between rates of exploitation on the stocks in the area.

INTRODUCTION

Attempts to estimate sea mortality of pink salmon (*Oncorhynchus gorbuscha*) from both natural causes and fishing have been presented by Neave (1953) and Hunter (1959). These estimates have lacked the benefit of any detailed knowledge of the rate of exploitation upon a particular stock, nevertheless survival from natural causes of roughly 5% was indicated as an average and fluctuations between 1.1 and 11.2% were indicated. These have been generally accepted by fishery workers as levels of natural sea survival for this species. Marking experiments on fry and fingerling in the central coastal area of British Columbia (Fig. 1) during 1961 and 1962 were designed to provide additional estimates of sea mortality, particularly to separate and ascertain differences between early mortality taking place while the juveniles remained in coastal waters and later mortality taking place in the open ocean habitat. The present purpose is to present an analysis of data acquired and the conclusions which may be drawn from these experiments.

[1]Received for publication January 24, 1964.

[2]Read at Ottawa (January 3, 1964) as part of a symposium, "Survival rates of anadromous salmon at successive life history stages", sponsored by Canadian Committee on Freshwater Fisheries Research.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

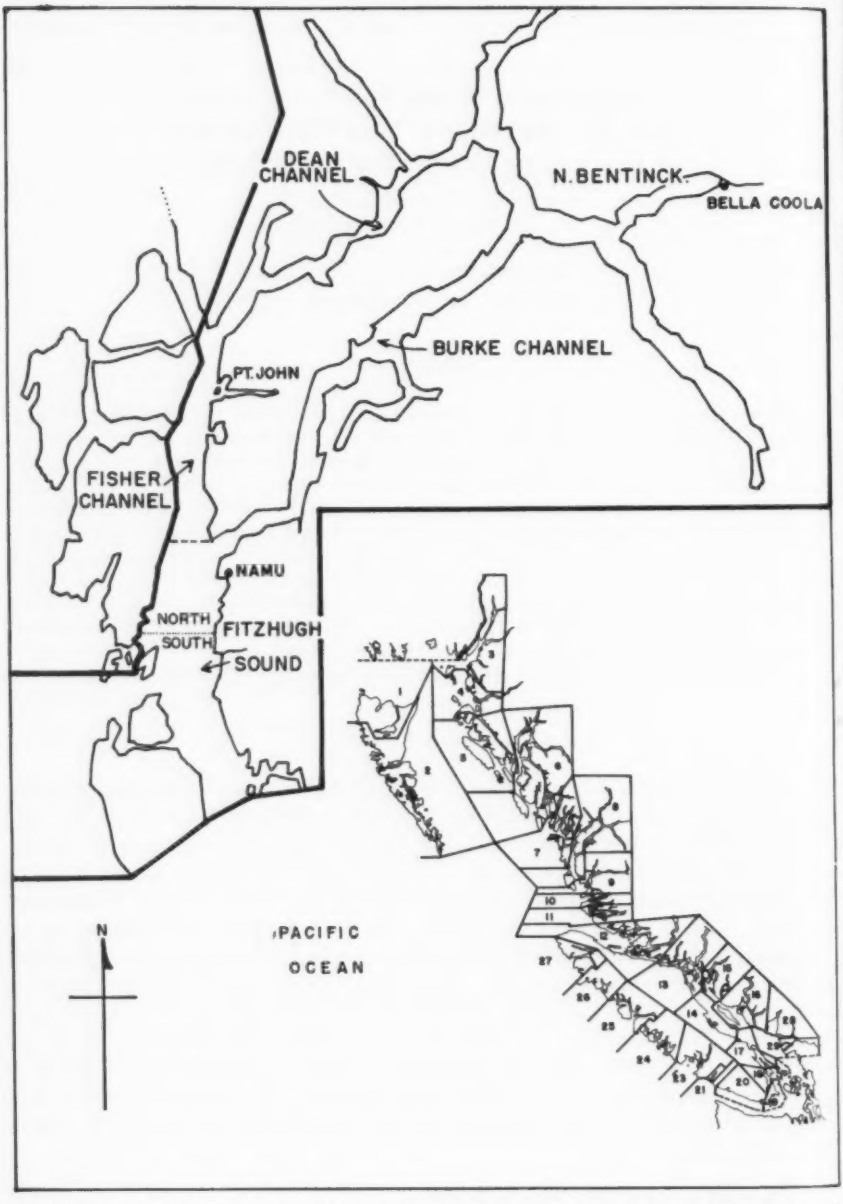


FIG. 1. A map of the coast of British Columbia divided into Statistical Areas with an enlarged plan of Area 8.

FRY MARKING

Pink salmon populations associated with Hook Nose Creek (Port John) have been under study for several years, and Port John facilities include a weir for the enumeration of both ascending adults and seaward migrating fry (Hunter, 1954, 1959). In 1960, 3165 adult pink salmon were passed above the weir; 420 were counted spawning in the intertidal waters below the weir. In February 1961, several redds were opened and the eggs and alevins were collected by holding a net downstream of the excavation. Of the total catches, 64.7% of the eggs and alevins obtained below the weir, and 65.5% of those above the weir, were alive. These data lead to the expectation that approximately 11.5% of the total fry production in Hook Nose Creek was from the intertidal zone. The total number of fry counted at the weir is estimated as 88.5% of the total production.

Enumeration of pink fry at the weir was complete with a single exception. On the evening of April 1 the weir was inundated for a short time resulting in a partial count of fry for that date. The count on March 31 was 17,000, and on April 2, 22,500. The partial count on April 1 was approximately 20,000 to which 20,000 has been arbitrarily added to provide a maximum estimate. The total estimate of fry above the fence for the season, March 15 to May 15, is 1,039,700. Error associated with the April 1 estimate is likely to have little effect on this total, amounting to less than 2% of the probable total fry output. Fry production below the weir is estimated at 140,700. Approximately 531,500 unmarked fry were released at the weir, i.e. 672,200 unmarked Hook Nose pink fry entered the sea.

During the period of out-migration, 480,800 fry were supposedly marked by removal of both ventral fins (BV) and released. These fish were not examined at the time of marking for an evaluation of the quality of the marks. During and subsequent to the marking period, however, samples of juvenile pink salmon which contained BV-marked fish were obtained from the waters of Fisher Channel and Fitz Hugh Sound. In total, 566 marked fish were recognized of which 2 were so poorly marked they were classified as "misses". Of the rest, 21 were classified as right ventral (RV) and 47 as left ventral (LV) marks. Assuming that such single marks and the "misses" would be present in the total population of marked individuals in the same proportions as in this sample, it is estimated that 479,000 effectively marked fish were released of which 421,500 would be recognized as BV, 17,700 as RV, and 39,800 as LV marks. On this basis it is estimated that a total of 1,153,000 Hook Nose Creek pink salmon fry entered the sea of which 479,000 or 41.5% were effectively marked and 674,000 were unmarked.

The recapture of marked fingerling as detailed above does not, of course, give any information on the proportion of fry which were supposedly marked but actually completely missed in the operation. This source of error is real[3] and has the effect of putting fewer marks at large than are used in subsequent calculations.

[3]In a more recent experiment with pink salmon fry, error in marking by removal of adipose and right ventral fins resulted in less than 0.2% of the total marked being classified as "misses".

Fish were anaesthetized before handling and held 12–24 hr before release. Very slight mortalities (<1%) were experienced and no correction is considered necessary for post-release marking mortality *per se*.

FINGERLING MARKING

During the period May 16–24, juvenile pink salmon were seined within a radius of 3 miles from Port John and transported to a floating facility in Port John for marking. Fish were held at the float, generally in excess of 6 hr, since immediate mortality due to catching and transportation was not negligible and was significantly increased if followed immediately by handling and marking. Fish were again anaesthetized before handling, held 24 hr after marking, and released. From this operation 37,476 fingerling marked by the removal of the adipose and right ventral fins (ARV) were released. Examination of a sample of 468 fish preserved from this marking led to the estimate that 7/468 or about 600 of the releases would probably be recognized as RV marks, and the remainder, about 36,900, as ARV marks on adults. The percentage of successful marks in this experiment is much higher than that for the fry (98.5% against 87.5%) and is attributable to the larger size of the fish marked (6.0 cm vs. 3.5 cm).

Prior to May 10, schools of fingerling were abundant along the shores of Fisher Channel. Fish were rarely sighted, and never in significant quantity, far from the beach. On May 10 a few schools were sighted off shore and by May 15, large schools were abundant completely across Fisher Channel. These appeared to be moving south. During the second marking period fish became increasingly scarce and could not be found in Fisher Channel by May 24, although they were still abundant in lower Burke Channel and in Fitz Hugh Sound. During this marking period an average of 1.14% of 38,058 fingerlings examined was recognized from the earlier fry marking. The majority of these recoveries came during the initial 7 days. The incidence of marks (BV + RV + LV) during the final 2 days of marking fell to about 0.5%. It may be concluded from these observations that the second marking took place during a period of emigration from the inside waters. The initial low incidence of BV marks (1–2%) is interpreted to indicate that a small fraction of the initial stock present was of Hook Nose Creek origin. The decline in this percentage of BV is explained as a further dilution of Hook Nose Creek pinks by stocks migrating through Fisher Channel from Dean Channel. As will be later substantiated by adult mark recoveries, the second marking was primarily of Dean Channel stocks rather than Hook Nose Creek or Bella Coola stocks.

For both markings only a single fish with naturally missing fins was noted: A Hook Nose Creek pink fry was found with the ventral fins and the pelvic bones missing. It was concluded that the incidence of naturally missing fins was not sufficiently large to influence the results of these experiments. A summary of releases is presented in Table I.

TABLE I. Estimated releases of pink salmon in Fisher Channel, 1960 brood year.

Source of fish	Central release date	Estimated number released				
		Marks				
		BV	LV	RV	ARV	Total
Fry, Hook Nose Creek	April 11, 1961	421,500	39,800	17,700		479,000
Fry, Hook Nose Creek (not marked)	April 11, 1961					674,000
Fingerlings, Port John–Fisher Channel	May 20, 1961			600	36,900	37,500
Total marks released:		421,500	39,800	18,300	36,900	516,500

MARK RECOVERY

During July and August 1962, technicians were stationed at various canneries in the Vancouver, Klemtu, and Prince Rupert areas. Catches originating from Statistical Areas 7 and 8 (Fig. 1, hereafter termed simply "Area") were routinely sampled, catches originating from other Areas were sampled where time allowed. The results of this search for marked fish are presented in Table II. Altogether 1,160,645 adult fish were examined and 5997 BV, 367 RV, 686 LV, and 184 ARV marks were recognized. Adults were also examined as they entered Hook Nose Creek and 2044 BV, 126 RV, 221 LV, and 2 ARV marks were found.

TABLE II. Number of fish examined on commercial catches and marks recognized by Statistical Areas.

Statistical Area	Number of fish examined	Marks recognized				
		BV	LV	RV	ARV	Total
5	5,931	0	0	0	0	0
6	44,284	6	4	1	0	11
7	32,535	236	8	2	2	248
8	901,174	4139	511	284	160	5094
9	983	0	0	0	0	0
10	1,245	0	0	0	0	0
11	100	0	0	0	0	0
12	6,220	0	0	0	0	0
Troll*	2,167	1	0	0	0	1
6 + 7	64,779	131	10	0	2	143
7 + 8	6,427	56	2	2	0	60
6 + 8	2,284	2	2	0	0	4
8 + 9	24,436	4	19	11	6	40
8 + 9 + 10	23,881	552	46	33	8	639
8 + 12	44,199	870	84	34	6	994
Total:	1,160,645	5997	686	367	184	7234

*West coast Vancouver Island.

Validity of Marks

The possibility exists that either fins had been lost from causes other than deliberate marking or regeneration of either fin occurred resulting in an altered or unrecognizable mark. Arguments against the occurrence of accidental marking are as follows. Firstly, technicians were instructed to note all missing fins, and no cases of fin mutilation were recorded other than those expected. Secondly, marks were not encountered in catches originating in Areas remote from the seaward approaches to Fitz Hugh Sound and Fisher Channel (Table II). Thirdly, any significant accidental marking of ventral fins in the sea would have applied equally to Hook Nose and non-Hook Nose stocks alike. Since the Hook Nose stock was already marked, any accidental marking would produce differences between the ratios of RV:LV:BV of the catch and that of the Hook Nose Creek escapement. Differences between these ratios are tested as set out in Table IIIa, resulting in $\chi^2 = 0.52$. The hypothesis of homogeneity among catch and escapement mark ratios need not be abandoned. These observations appear to preclude the occurrence of any significant accidental marking.

Fin regeneration remains as a possible source of error in these data. If the assumption is made that the ratios of BV:RV:LV, as determined from the fingerling sample, are identical (without sampling error) so that of the BV marked population at the time of marking, then significant changes in these ratios occurred during the time spent in the sea. In Table IIIb adult ratios (catch + escapement) are compared with ratios expected on the basis of the

Table III. Tests for significance of differences among sample ratios of BV:RV:LV marks.

a. Hypothesis of homogeneity among catch and escapement mark ratios.

			BV	RV	LV	Total
Adult catch	observed	(X)	5997	367	686	7050
	expected	(m)	6005	368	677	
	deviation	(x)	−8	−1	+9	
Adult escapement		(X)	2044	126	221	2391
		(m)	2036	125	230	
		(x)	+8	+1	−9	
Total:			8041	493	907	9441

$\chi^2 = 0.52$.

b. Hypothesis of no change in mark ratios from fingerling to adult.

			BV	RV	LV	Total
Fingerling observed			496	21	47	564
Adult	observed	(X)	8041	493	907	9441
	expected		8303	351	787	
	deviations		−262	+142	+120	

$\chi^2 = 84$.

fingerling sample. Apparently about 3% of the double fin marks may have been altered to single fin marks. A χ^2 value of 84 is obtained. Clearly any hypothesis of sameness is suspect.

A model was employed depicting the effects of fins regenerating, embodying the assumptions:

(a) that the probability of a left ventral fin regenerating was equal to that of a right ventral fin regenerating, and

(b) that probabilities of each fin regenerating in a double fin mark were independent.

Trial values for the probability of a fin regenerating were applied to the mark release estimates and the results compared with the observed adult recoveries by χ^2. For example, if a trial value of 2% is chosen, there are four possible events for a fish marked BV. These are: (1) the fish retains both ventral marks with the probability of $(0.98)^2$ or 0.9604, (2) it regenerates a left ventral but not a right ventral with a probability of (0.02)(0.98) or 0.0196, (3) it regenerates a right ventral but not a left ventral which again has a probability of 0.0196, and (4) it regenerates both right and left ventrals and the probability of this event occurring is $(0.02)^2$ or 0.0004. The resulting distribution of marks is given in Table IV. Using these results as the expected ratios, a χ^2 value of 1.569 is obtained. The distribution of χ^2 as a function of the probability of a fin regenerating is approximately parabolic, therefore, three sets of trial values were used to solve for the probability of a fin regenerating which provides the minimum χ^2. This value is 0.0179, which results in a theoretical mark ratio closely approximating the observed values ($\chi^2 = 0.226$). It may be noted that error from fin regeneration at a rate of 2% resulted in the complete obliteration of only 28 marks per 10,000. Error from this source, while it is considered to be small, has the effect of putting fewer marked fry at large than were reported.

TABLE IV. Calculation of mark ratio changes under the hypothesis of 2.0% fin regeneration and comparison with observed return ratio.

Reduction coefficient	BV	RV	LV	Not marked	Total
Original	8795	372	833		10,000
0.0196	−172	+172			
0.0196	−172		+172		
0.0004	−4			+4	
0.0200		−7		+7	
0.0200			−17	+17	
After regeneration	8447	537	988	28	10,000
Observed	8041	493	907		9441
Expected	7997.2	508.4	935.4		9441.0
Deviations	+43.8	−15.4	−28.4		

$\chi^2 = 1.569$.

Alternatively, the mark ratios obtained from the fingerling samples may be treated as samples of the marked population along with those of the catch and of the escapement and tested for homogeneity. This calculation is set out in Table V. A χ^2 value of 4.2314 (d.f. = 4; $0.30 < P < 0.50$) is obtained indicating that all three samples ratios might have been drawn from the same parent population. From these considerations it is not possible to establish that fin regeneration actually occurred. If it did, under the assumptions employed in the model, it was at a very low rate and had the main effect of reducing the BV marks to RV and LV and a negligible effect of reducing the number of recognizable marks out.

From data presented earlier, it was expected that for each ARV mark recovered there would, on the average, be 0.0152 RV marks recovered from the second marking. Since 184 ARV marks were recovered (Table II) about 3 RV marks (184×0.015) would be anticipated from that marking. Any bias introduced by assuming that all single fin marks result from the first (both ventral) marking has only a minor effect on the tests which follow and is therefore ignored.

TABLE V. Test for significance of differences among the sample ratios of BV:RV:LV marks.

			BV	RV	LV	Total
Fingerling	observed	(X)	496	21	47	564
	expected	(m)	481.2	29.0	53.8	
	deviation	(x)	+14.8	−8.0	−6.8	
Adult catch		(X)	5997	367	686	7050
		(m)	6015.6	362.2	672.2	
		(x)	−18.6	+4.8	+13.8	
Adult escapement		(X)	2044	126	221	2391
		(m)	2040.2	122.8	228.0	
		(x)	+3.8	+3.2	−7.0	
Total:			8537	514	954	10,005

$\chi^2 = \Sigma x^2/m = 4.2314$, d.f. = 4
$0.30 < P < 0.50$.

INTERPRETATION OF MARK RECOVERIES

Many of the loads examined contained fish originating in several Areas which led to uncertainty in the interpretation of marked to unmarked ratios. A further complication became evident when the returns of the two markings were compared. Early in the season ARV marks were approximately half as numerous as BV marks, but as the season progressed this ratio changed grossly in favour of BV marks. Furthermore, landings of fish originating from the Bella Coola gill-net fishery contained very few marks and even these cannot be determined with certainty as actually having been caught in the Bella Coola area because of the mobile nature of both fishing boats and packers. Finally, while there was no conscious effort made to sample only those loads containing

marked fish, any such bias would cause serious over-estimation of the total catch of marked fish. To minimize these effects catch and mark data were classified according to both fishing week and sub-area before calculation of mark returns and totalling.

Area 8 was divided into 4 sub-areas as shown in Fig. 1, and the recovery period into fishing weeks as detailed in Table VI. Within each sub-area the decimal fraction of the sample marked BV and ARV was calculated or estimated as given in Tables VI and VII. Area 8 pink salmon catches, as reported to the Department of Fisheries, are given by weekly totals in the bottom of Table VIII. The Area Fishery Inspector, from daily radio contacts with fish packers, divided the daily catch as originating either in the Bella Coola gill-net fishing area or in the rest of Area 8 (Fisher–Fitz Hugh) and accounted for over 9 million of the 12 million fish catch in this manner. Using these data the portion of the total catch originating in the Bella Coola area by weekly periods has been estimated as shown in Table VIII. Cannery records and packer log books were obtained to supplement this and the sampling records to determine the collection points and loads of the packers. Where loads originated from more than one sub-area they were not included. Loads of fish originating from a particular sub-area were assumed to have been caught there. A totalling of these data leads to the estimation of the percentage of Area 8 catch which might be assigned to each sub-area during each weekly fishing period. These estimates are also given in Table VIII. Multiplication of these values by the decimal fractions of samples found to be marked (Tables VI, VII) yields the estimates of marked fish caught by the fishery given by the middle and lower lines of each sub-section in Table VIII. On these bases it is estimated that the total catch of marked fish in Area 8 was 47,239 BV and 2478 ARV.

Catch of Hook Nose Creek Pink Salmon

The entire count of pinks entering Hook Nose Creek in September and October was 8288 of which 2391 were marked BV, RV, and LV and 2 were marked ARV. Assuming no selectivity of fishing gear for marked members, then

$$(5{,}897/2{,}391)\ 47{,}239 \approx 116{,}500$$

is the estimated catch of unmarked Hook Nose Creek pinks within Area 8.

Both ventral marks were also found in catches originating from Areas 5, 6, and 7 as shown in Table II. Preliminary catch figures of the Department of Fisheries are, for Area 6 — 3,668,841 and Area 7 — 1,162,259. The estimate of the Area 6 catch of BV marks is then

$$(11/44{,}284)\ 3{,}668{,}841 \approx 900$$

and for Area 7

$$(246/32{,}535)\ 1{,}162{,}259 \approx 8800.$$

The catch of unmarked Hook Nose Creek pink salmon is estimated by

$$(900)\ (5897/2391) \approx 2200$$

for Area 6 and by

$$(8800)\ (5897/2391) \approx 21{,}700$$

TABLE VI. Estimation of fraction of catch marked ARV by sub-area and fishing week, 1962 Area 8 pink salmon.

Sub-area	July – August								Totals
	8–14	15–21	22–28	29–4	5–11	12–18	19–25	26+	
South Fitz Hugh Sound	...	7[a]	3	3	1	0	...	...	14
	...	34,655	11,175	10,178	16,297	20,874	0	0	93,179
	...	.000202	.000268	.000295	.000061	0	(0)[b]	(0)	.000150
North Fitz Hugh Sound	2	10	16	13	9	1	2	...	53
	32,741	49,043	69,103	46,926	37,436	20,247	14,611	0	270,107
	.000061	.000204	.000231	.000277	.000240	.000049	.000137	(0)	.000196
Fisher Channel	...	6	12	12	9	1	2	0	42
	...	18,553	24,715	48,065	27,287	20,073	7,204	9,455	155,352
	...	.000323	.000486	.000250	.000330	.000050	.000278	0	.000270
Bella Coola	...	...	0	0	1	...	...	...	1
	...	0	12,206	17,805	11,693	0	0	0	41,704
	...	(0)	0	0	.000086	(0)	(0)	(0)	.000024
Area 8 mixed loads	5	18	15	9	0	1	2	...	50
	13,025	97,171	108,217	67,175	15,279	30,080	9,885	0	340,832
	.000384	.000185	.000139	.000134	0	.000033	.000202	(0)	.000147
Totals:	7	41	46	37	20	3	6	0	160
	45,766	199,422	225,416	190,149	107,992	91,274	31,700	9,455	901,174
	.000153	.000206	.000204	.000195	.000185	.000033	.000189	0	.000178

[a]For each sub-area: top line gives number of marks found, middle line the number of fish examined, bottom line the decimal fraction of the sample that was marked.

[b]Figures in parantheses are estimates based upon information for adjoining sub-areas and dates.

TABLE VII. Estimation of fraction of catch marked BV by sub-area and fishing week, 1962 Area 8 pink salmon.

	July – August								
	8–14	15–21	22–28	29–4	5–11	12–18	19–25	26+	Total
South Fitz Hugh Sound	...	19[a]	16	23	116	183	...	...	357
	...	34,655	11,175	10,178	16,297	20,874	0	0	93,179
	...	.000548	.001431	.002260	.007118	.008767	(.008)[b]	(.007)	.003831
North Fitz Hugh Sound	7	10	60	125	405	404	108	...	1,119
	32,741	49,043	69,103	46,926	37,436	20,247	14,611	0	270,107
	.000213	.000204	.000868	.002664	.010818	.019954	.007392	(.007)	.004143
Fisher Channel	...	14	34	126	688	1,154	337	340	2,693
	...	18,553	24,715	48,065	27,287	20,073	7,204	9,455	155,352
	...	.000755	.001376	.002621	.025213	.057490	.046780	.035960	.017335
Bella Coola	...	...	0	0	6	...	...	...	6
	...	0	12,206	17,805	11,693	0	0	0	41,704
	...	(0)	0	0	.000513	(0)	(0)	(0)	.000144
Area 8 mixed loads	6	31	52	90	82	368	132	...	761
	13,025	97,171	108,217	67,175	15,279	30,080	9,885	0	340,832
	.000461	.000319	.000481	.001340	.005367	.012234	.013354	(.013)	.002233
Totals	13	74	162	364	1,297	2,109	577	340	4,936
	45,766	199,422	225,416	190,149	107,992	91,274	31,700	9,455	901,174
	.000284	.000371	.000719	.001914	.012010	.023106	.018201	.035960	.005477

[a]For each sub-area: top line gives number of marks found, middle line the number of fish sampled and bottom line the decimal fraction of the sample that was marked.

[b]See Table VI, footnote b.

TABLE VIII. Estimated catch of marked fish by sub-areas and fishing weeks, 1962 Area 8 pink salmon.

	July – August								
	8–14	15–21	22–28	29–4	5–11	12–18	19–25	26+	Totals
Southern Fitz		1,545,106[a]	1,294,680	529,115	129,732	92,272	9,832	2,293	3,603,030
Hugh Sound		847	1,853	1,196	923	809	(75)	(16)	5,719
		312	347	156	8	0	(0)	(0)	823
Northern Fitz	353,939	819,990	1,975,418	539,537	361,618	178,236	61,728	60,685	4,351,151
Hugh Sound	82	167	1,715	1,437	3,912	3,557	456	(425)	11,751
	22	167	456	149	87	9	8	(0)	898
		187,672	739,030	626,151	281,573	226,128	131,101	13,805	2,205,460
Fisher Channel		142	1,017	1,641	7,099	13,000	6,133	496	29,528
		61	359	157	93	11	36	0	717
	32,948	0	621,850	579,930	469,593	224,545	54,792	7,748	1,991,406
Bella Coola	(0)		0	0	241	(0)	(0)	(0)	241
	(0)		0	0	40	(0)	(0)	(0)	40
	386,887	2,552,768	4,630,978	2,274,733	1,242,516	721,181	257,453	84,531	12,151,047
Total Area 8	82	1,156	4,585	4,274	12,175	17,366	6,664	937	47,239
	22	540	1,162	462	228	20	44	0	2,478

[a]For each sub-area: top line gives estimated catch, middle line estimated BV marks, and bottom estimated ARV marks in catch.

for Area 7. These values add further refinement and are included in the estimates of the rates of exploitation, natural survival, and instantaneous mortality rates as shown in Table IX. Approximately 22% of the entering unmarked fry population survived to return as the adult population. Of these the fishery took approximately 95%. The total instantaneous natural mortality rate of marked fish was 1.37 times that of the unmarked population.

TABLE IX. Summary of computed survival statistics of 1960 brood-year Hook Nose Creek pink salmon.

	Marked	Unmarked	Total
Fry entering the sea[a]	479,000	674,000	1,153,000
Catches[b] Area 8	47,200	116,500	163,700
Catches[b] Area 7	8,800	21,700	30,500
Catches[b] Area 6	900	2,200	3,100
Catches[b] Total	56,900	140,400	197,300
Escapement[a]	2,800	6,800	9,600
Return[c]	59,700	147,200	206,900
Rate of exploitation (u)[d]	0.954	0.954	0.954
Natural survival (S)[e]	0.125	0.218	...
Instantaneous natural mortality rate (i)[f]	2.08	1.52	...

[a]Estimated from fence counts at tidewater on Hook Nose Creek plus tidal spawners.
[b]Estimated from area or sub-area marked/unmarked fractions in catches sampled.
[c]Catch + escapement.
[d]Catch/return.
[e]Return/fry.
[f]$S = e^{-i}$ for $t = 17$ months.

INITIAL MORTALITY RATES

Recoveries of ARV marks are given in Tables II and IV. The estimate of total ARV marks in the Area 8 catch is given in Table VI. Direct information is lacking on the escapement fraction of this group and rate of exploitation and survival cannot be computed.

It is here proposed that the expression

$$C_t = N_O u S_m e^{-mtq} \tag{1}$$

is representative of the marked populations. Here N_O denotes the population of marked fish at the time of marking; u denotes the seasonal rate of exploitation; S_m denotes the short-term survival rate from the effects of marking; m denotes the long-term effects of marking on the instantaneous mortality rate, q; t denotes the time period elapsing between marking and recovery; C_t denotes the number of marked survivors taken by the fishery at time t. Where two sets of data are available equation (1) may be used in a set of simultaneous equations a and b leading to the expresion

$$e^{mq\,(t_a - t_b)} = \frac{C_{tb}\ N_{Oa}\ u_a\ S_{ma}}{C_{ta}\ N_{Ob}\ u_b\ S_{mb}} \tag{2}$$

where it is assumed that $q_a = q_b$. From (2) mq can be evaluated if u_a/u_b and S_{ma}/S_{mb} are known.

In the present case the two lots of fish (BV and ARV) were held under observation after marking and the immediate effects of excitement, handling and wounding were substantially over at release. Thus the fraction S_{ma}/S_{mb} may be approximated as 1. A real difficulty arises in evaluating the fraction

u_a/u_b. Both groups were fished by the same fleet in July and August 1962. If both groups had been subjected to identical fishing rates then the fraction C_{tb}/C_{ta} should be relatively constant throughout the season and from area to area. Values of this fraction are compared in Table X. Here C_{ta} = BV recoveries and C_{tb} = ARV recoveries. This comparison shows that relatively great differences in weekly rates of exploitation existed and it is concluded that the two marked populations were not subject to identical seasonal rates of exploitation. Consequently we neither can evaluate the fraction u_a/u_b nor assume equality from these data. It can only be concluded that the two marked populations were subject to totally dissimilar rates of exploitation and the results are, therefore, not usable for estimating the natural mortality rate during the time interval between markings.

DISCUSSION

A first reaction to the estimate of sea survival from natural mortality factors (Table IX) could be one of incredulity, for 22% is approximately twice the highest estimate by Hunter (1959) for this same stock and some 4–5 times that of the generally accepted average figure (Neave, 1953). On the other hand, data contributing to the present estimate are substantial and include estimates of the specific effects of the fishery which were unknown to both Hunter and Neave. The estimate of the rate of exploitation also seems high for both Neave (1953) and Hunter (1959) have stated that, based on catch and escapement estimates for rather broad areas, $u \approx 65\%$. Sources of error from mis-marking and fin regeneration tend to minimize the estimates of return and rates of exploitation. The total marks recovered, 4936 BV:160 ARV or a ratio of 308.5:1 was substantially altered by the correction for area and time distribution so that the estimated catch of marks was 47,239 BV:2478 ARV or 190.5:1. Thus the estimate of the catch of BV marks was minimized. These all have the effect of *reducing* estimates of survival and rate of exploitation.

The escapement of fish into the Bella Coola system (Fig. 1) in 1962 has been variously estimated at 3–5 million, and the Bella Coola contribution to the catch was probably of the order of 11–12 million. The rate of exploitation for that system, then, was about 69–80%. It has already been demonstrated that fish predominantly from Dean Channel (the ARV-marked group) were not subject to the same fishing mortality rates as the Hook Nose Creek stock. Both Dean Channel and Bella Coola stocks moved through Fitz Hugh Sound. The Dean Channel stock also arrived in Fisher Channel by way of Milbanke Sound but apparently did not remain in the Fisher–Fitz Hugh area. The Bella Coola stock must move into Burke Channel (of which the southwestern half was closed to fishing) but was again fished to a lesser extent in Upper Burke Channel and North Bentinck Arm. The Hook Nose Creek stock remained in the fishing area of Fisher–Fitz Hugh Sound and approaches during the major part of the fishing season. The mark recoveries suggest that the Hook Nose Creek stock entered early and was available generally throughout the Fisher Channel–Fitz Hugh Sound area for a protracted period of time, during which fishing was conducted on the Bella Coola stock which was moving through the fishing area into a protected area. These migration patterns resulted in differences in availability to

TABLE X. Comparison of BV and ARV marks recovered and the values of ARV/BV.

		July – August								
		8–14	15–21	22–28	29–4	5–11	12–18	19–25	26+	Totals
South Fitz Hugh Sound	ARV	...	7	3	3	1	0	...	...	14
	BV	...	19	16	23	116	183	...	...	357
	ARV/BV	...	.3684	.1875	.1304	.0086	<.0055	...	...	.0392
North Fitz Hugh Sound	ARV	2	10	16	13	9	1	2	...	53
	BV	7	10	60	125	405	404	108	...	1,119
	ARV/BV	.2857	1.0000	.2667	.1040	.0222	.0025	.0185	...	.0474
Fisher Channel	ARV	...	6	12	12	9	1	2	0	42
	BV	...	14	34	126	688	1,154	337	340	2,693
	ARV/BV	...	.4286	.3529	.0952	.0131	.0009	.0059	<.0059	.0156
Bella Coola	ARV	...	...	0	0	1	...	...	...	1
	BV	...	...	0	0	6	...	...	...	6
	ARV/BV	...	...	...	...	.1667	...	...	...	.1667
Area 8 mixed loads	ARV	5	18	15	9	0	1	2	...	50
	BV	6	31	52	90	82	368	132	...	761
	ARV/BV	.8333	.5806	.2885	.1000	<.1220	.0027	.0152	...	.0657
Totals	ARV	7	41	46	37	20	3	6	0	160
	BV	13	74	162	364	1,297	2,109	577	340	4,936
	ARV/BV	.5385	.5540	.2840	.1016	.0154	.0014	.0104	<.0059	.0324

the fishery and may explain the differences in seasonal rates of exploitation. This explanation is reinforced by the observation that approximately 29,500 of the 47,200 or 62.5% of the estimated BV marks caught came from Fisher Channel. Had Fisher Channel been closed to fishing the rate of exploitation on the Hook Nose Creek stock would have been lower, perhaps as low as 38%. A situation similar to this must have prevailed on the Dean Channel stocks.

TABLE XI. Comparison of marine survival of 1947–60 brood years, Hook Nose Creek pink salmon, fence counts only.

Brood years	Fry entering the sea	Adults entering the stream	Marine survival
1947	20,516	1,070	5.2
1948	60,841	1,857	3.1
1949	52,399	1,670	3.2
1950	232,636	8,685	3.7
1951	237,963	1,599	0.7
1952	1,212,798	31,402	2.6
1953	199,966	1,310	0.7
1954	898,481	21,650	2.4
1955	85,737	2,333	2.7
1956	445,798	6,109	1.4
1957	59,649	1,500[a]	2.5
1958	743,465	3,165	0.4
1959	203,437	354	0.2
1960	543,503[b]	5,897	1.1

[a]Estimated, fence not operated.
[b]Includes only unmarked fry released at the fence to be consistent with other figures.

It is also informative to extend the observations of marine survival presented by Hunter (1959) to include recent brood years of the Hook Nose stock. These are presented in Table XI. These recorded total marine survival figures (natural × fishing) are characterized by both a declining trend and severe fluctuations. The escapement of the 1959 brood year in 1961 was the lowest value obtained and while no data are available to separate natural and fishing mortality the escapement was much better within Area 8 as a whole. It is suggested that the series of data presented in Table XI reflect severe differences in fishing intensity upon that particular stock. With these arguments the estimates of catch and marine natural mortality rates derived for the 1960 brood year are entirely credible.

ACKNOWLEDGMENTS

The data presented in this paper largely resulted from the faithful execution of field duties by competent technicians. Chief among these was Mr Ralph C. Wilson, of the Board's Biological Station at Nanaimo. Use of these data and the ensuing conclusions have received the excellent criticisms of Dr Peter A. Larkin, Dr M. P. Shepard, and Mr F. C. Withler also of the Biological Station, Nanaimo, and of Dr G. J. Paulik of the University of Washington.

REFERENCES

HUNTER, J. G. 1954. A weir for adult and fry salmon under conditions of extremely variable run-off. *Canadian Fish Culturist*, No. 16, pp. 1–7.

1959. Survival and production of pink and chum salmon in a coastal stream. *J. Fish. Res. Bd. Canada*, **16**(6): 835–886.

NEAVE, FERRIS. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. *J. Fish. Res. Bd. Canada*, **9**(9): 450–491.

Seasonal Variations in the Sterol, Fat and Unsaponifiable Components of Scallop Muscle[1,2]

By D. R. Idler, T. Tamura[3] and T. Wainai[3]

Fisheries Research Board of Canada
Technological Research Laboratory, Halifax, N.S.

ABSTRACT

The total fats, unsaponifiable material, provitamins D, and sterols were determined on monthly samples of male and female sea scallop, *Placopecten magellanicus* (Gmelin). During the pre-spawning period (August), total fat, unsaponifiable, and sterol levels were low indicating an active transfer of these materials to the gonad tissue. During the retarded growth period (February, March), the fat content of the muscle decreased but there was a compensating increase in the unsaponifiable and sterol content of the total fat. The composition of the sterol fractions was determined by gas chromatography. The principal sterol components of the scallop muscle were found to be 22-dehydrocholesterol, cholesterol, brassicasterol, and 24-methylenecholesterol. Changes in the composition of the sterols were not as extreme as those reported in the literature for some other shellfish. However, variations in the cholesterol and 24-methylenecholesterol content of the scallop muscle suggested a relationship in the metabolism and biosynthesis of these sterols. There were no obvious differences in the composition of the muscle of male and female scallops.

INTRODUCTION

The sterols of marine invertebrates are complex mixtures of closely related compounds that cannot be separated into their components by conventional chemical methods. A definitive analysis of the composition of these mixtures is complicated further by the variations in composition found in samples of sterols isolated from different samples of the same species. In his review of the comparative biochemistry of sterols, Bergmann (1962) pointed out that the significance of the fluctuation in the sterol composition of bivalves was not understood. Toyama and Tanaka (1954) reported the absence of a di-unsaturated sterol in a sample of unsaponifiable material isolated from a pelecypod, *Corbicula leana*, although other samples of sterols isolated from the same species contained the sterol in quantities sufficient to identify it as brassicasterol. During the course of investigation of the sterol composition of the muscle of the scallop (Tamura *et al.*, 1964; Wainai *et al.*, 1964) some variation in the quantities of individual sterols was observed.

Gas–liquid chromatography has provided a method of analysis rapid and accurate enough to apply to a study of variations in composition of a number of samples of sterol mixtures. The experiment described here was designed to

[1]Received for publication June 23, 1964.
[2]This investigation was supported by a research grant of the National Institutes of Health, U.S. Public Health Service.
[3]Present address: Nihon University, Tokyo, Japan.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

determine if the changes noted in the composition of the sterols of the scallop, *Placopecten magellanicus* (Gmelin), were seasonal in nature or were related to the sex of the animal.

MATERIALS AND METHODS

Samples of sea scallops were obtained each month from April 1962 until April 1963 from a commercially operated scallop dragger fishing on Georges Bank, off the Nova Scotia coast. The live scallops were brought to shore at Lunenburg, Nova Scotia, shucked, separated when possible into two groups according to sex, and the adductor muscle was frozen immediately for shipment to the laboratory.

Extraction of Fats

Approximately 2 lb of scallop meat was extracted by blending for 5 min with 3.25 liters of absolute isopropanol, then 3.0 liters of 80% aqueous isopropanol, and finally 2.0 liters of absolute isopropanol (Dambergs, 1959). The extracts were combined and concentrated to 2 liters by a vacuum evaporator (Precision Laboratory Evaporator No. 620A, Precision Scientific Co., Chicago, Ill.) and then to 200 ml with a flash evaporator. Evaporating temperatures were maintained between 50 and 60°C. The concentrated extract was added to 2 liters of ether and the water solubles removed by washing thoroughly with water. The ether extract was evaporated *in vacuo*; benzene was added to co-distil the water from the residue. The scallop fats were then dried to constant weight over phosphoric anhydride in a vacuum desiccator.

Preparation of Crude Sterols

The fats obtained from each sample were dissolved in 30 ml 2*N* methanolic KOH and refluxed gently for 1 hr under nitrogen. The unsaponifiable matter, obtained in the usual manner by ether extraction, was dried under vacuum at low temperature and weighed. Eighty milligrams of the unsaponifiables was dissolved in 40 ml 90% ethanol, to which 10 ml of a saturated solution of digitonin in 90% ethanol was added. The mixture was allowed to stand at room temperature overnight. The precipitate was collected, washed with 10 ml 90% ethanol, then 3 times with 10 ml distilled water and dried *in vacuo*. The sterols were recovered from the sterol digitonide by treatment with pyridine according to the method of Bergmann (1940). The final crude free sterol preparation was dried in an Abderhalden dryer and weighed.

Determination of $\Delta^{5,7}$-Sterols

The $\Delta^{5,7}$-sterol (provitamin D) content of the total sterol fraction was determined by ultraviolet absorption (Glover *et al.*, 1952).

Gas Chromatography of Scallop Sterols

The apparatus used was a Barber-Colman Model 10 with an argon ionization detector and glass column (4 mm I.D., 6 ft in length). The column was packed with 5% SE-30 on Anakrom ABS 70/80 mesh (Analytical Engineering Laboratories). The argon pressure was 30 psi and the temperatures (°C) used were:

column, 230°; flash heater, 310°; and detector cell, 275°. The column was equilibrated before use and analyses of all samples were done on the same column. Peak areas on the chromatogram were measured by a Disc Co. integrator and assumed to be equal to weight per cent.

RESULTS

The date of capture and the yield of fats, unsaponifiable matter, sterols, and $\Delta^{5,7}$-sterols as determined on each sample of scallop muscle are listed in Table I. In four instances the male and female samples were not analysed separately as the samples received by the laboratory had not been separated prior to freezing. The analysis of the other eight samples showed no differences in composition of the muscle of male and female scallops. The monthly variation in fat content of the muscle of male and female scallop is illustrated in Fig. 1. In the late summer (August), the yield of fat was low and contained a low percentage of unsaponifiable material and sterols whereas the low fat content found in the late-winter samples was offset by high unsaponifiable and sterol values.

TABLE I. Weight per cent of total fats and unsaponifiable materials of monthly samples of scallop muscle (M = male, F = female).

Date of capture		Fats (% of meat)	Unsaponifiable material (% of fats)	Unsaponifiable material (% of meat)	Sterols (% of fats)	Sterols (% of meat)	$\Delta^{5,7}$-sterols (% of sterols)
Apr. 4, 1962		0.85	18.8	0.16	12.1	0.10	0.59
May 4		1.04	14.0	0.15	10.6	0.11	3.0
June 4	M	1.04	14.1	0.15	12.1	0.13	0.73
	F	1.06	14.7	0.16	11.1	0.12	0.41
June 29	M	1.09	14.3	0.16	9.5	0.10	0.65
	F	0.94	14.3	0.13	9.4	0.088	0.53
Aug. 9		0.67	10.7	0.072	7.1	0.048	0.66
Aug. 30		0.60	16.6	0.10	11.6	0.070	1.00
Oct. 15	M	0.96	15.2	0.15	13.0	0.13	1.06
	F	0.90	16.4	0.15	13.9	0.13	1.12
Nov. 6	M	0.88	18.1	0.16	14.2	0.12	1.52
	F	0.71	21.6	0.15	17.4	0.12	1.57
Dec. 20	M	0.97	14.9	0.14	12.6	0.12	1.18
	F	0.99	14.6	0.14	12.7	0.13	1.56
Jan. 25, 1963	M	0.72	19.6	0.14	17.3	0.12	1.32
	F	0.76	19.5	0.15	17.2	0.13	1.52
Mar. 8	M	0.64	19.8	0.13	18.1	0.12	1.12
	F	0.67	19.7	0.13	17.8	0.12	1.80
Apr. 23	M	0.69	19.7	0.14	16.9	0.12	0.76
	F	0.73	16.8	0.12	14.8	0.11	0.94

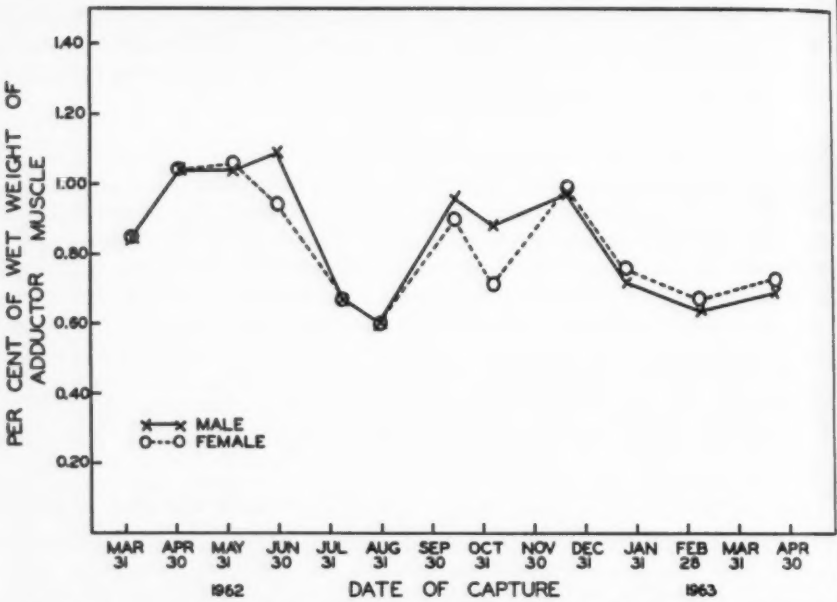


FIG. 1. Seasonal variation in the total fat content of the muscle of male and female scallop. Samples in March, April, and August contained both sexes.

Gas–liquid chromatography of the total sterol fractions separated them into seven components, four of which accounted for over 80% of the total. The peak areas of the chromatogram were designated by a letter according to their column retention time (r_c) relative to cholestane. Wainai *et al.* (1964) identified the components represented by the peak areas of the gas chromatogram as follows: X_1, C_{26} compounds; A, 22-dehydrocholesterol (Tamura *et al.*, 1964); B, cholesterol and a small amount of cholestanol; C, brassicasterol or its C_{28}-stereoisomer; D, 24-methylenecholesterol (Fagerlund and Idler, 1956) as the main component (over 85%) and a C_{28}-sterol tentatively identified as Δ^5-ergosterol; X_2, a C_{29}-sterol, probably stigmasterol; E, a mixture of unsaturated C_{29}-sterols. The total composition of the sterols of the monthly samples of scallop muscle is given in Table II. The variations in monthly values for the main components, 22-dehydrocholesterol, cholesterol, brassicasterol, and 24-methylene cholesterol (A, B, C, D) are shown in Fig. 2.

DISCUSSION

The scallops collected for this study were taken from the same sea beds, as differences in chemical composition within a species of marine invertebrate may depend in part on the locality of its native waters. The effect of exogenous sterols in the diet upon the endogenous sterols of shellfish is not clearly understood. It has been established that molluscs, unlike some insects, are able to synthe-

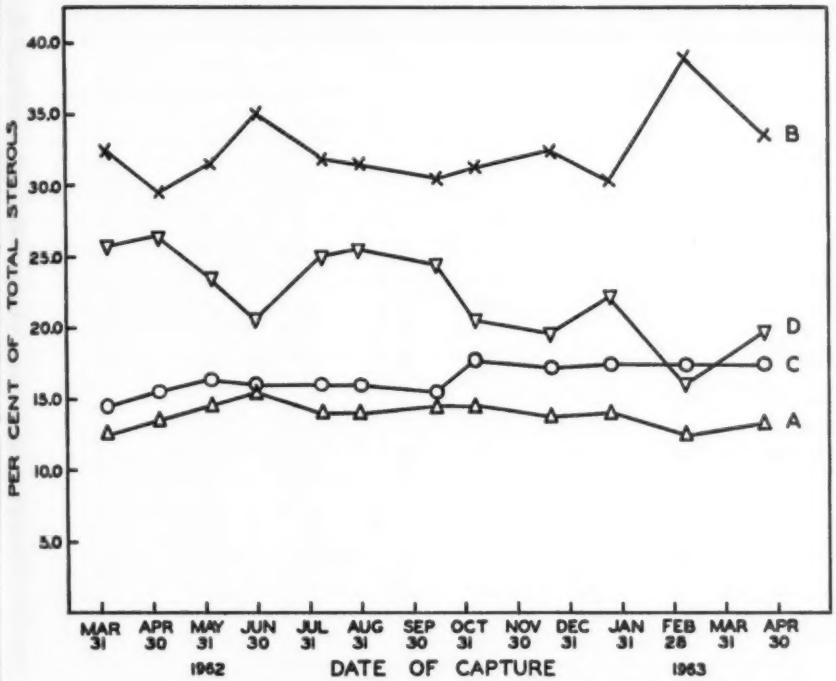


FIG. 2. Seasonal variation in the composition of the total sterols of scallop muscle. The principal sterols represented here by A, B, C, D were identified as 22-dehydrocholesterol, cholesterol, brassicasterol, and 24-methylenecholesterol, respectively. The percentage values are the average of values obtained for male and female scallop samples.

size sterols but there is some evidence that exogenous sterols are converted to the endogenous sterols typical of the animal. *In-vivo* studies by Fagerlund and Idler (1960) showed that a starfish, a species in which the sterols are characteristically unsaturated at C_7, converted an injested Δ^5-sterol, cholesterol, to Δ^7-cholestenol.

The decrease in the total fat content of the muscle found in the late-summer and late-winter samples is probably a result of the annual cycle in the life history of the scallop. The gonads of both sexes begin development in the early spring and by late summer have attained a weight equal to 60% of the adductor muscle (N. Bourne, private communication). The spawning of scallops on Georges Bank has been reported by Posgay (1958) to occur in late September. The rate of growth of the scallop is affected by environmental conditions; annual growth rings in the shell indicate a cessation of growth during the cold winter months (Stevenson and Dickie, 1954). It is interesting to note that if the fat content of the muscle is a criterion, then the recovery of the scallop from spawning and from adverse environmental conditions is relatively rapid.

TABLE II. Weight per cent of component sterols of fats of scallop muscle as determined by gas chromatography (r_c = column retention time of peak areas relative to cholestane). (M = male, F = female.)

Date of capture		Peak areas[a] X_1 r_c: 1.26	A 1.82	B 2.02	C 2.30	D 2.66	X_2 3.2	E 3.5
		%	%	%	%	%	%	%
Apr. 4, 1962		4.1	12.6	32.5	14.5	25.7	2.5	9.2
May 4		5.2	13.5	29.4	15.7	26.4	1.7	8.0
June 4	M	6.4	14.2	33.0	15.7	22.8	1.7	6.1
	F	6.1	14.8	30.0	16.9	24.1	1.9	6.0
June 29	M	6.9	15.4	33.4	16.0	20.7	1.9	5.6
	F	6.1	15.8	36.8	15.8	20.4	1.1	3.7
Aug. 9		6.1	14.1	31.8	15.9	25.0	1.4	5.7
Aug. 30		5.4	14.0	31.5	15.8	25.4	1.6	6.3
Oct. 15	M	7.0	15.2	30.8	15.2	24.0	1.2	6.6
	F	6.0	14.0	30.4	15.6	25.2	1.7	7.0
Nov. 6	M	7.4	14.3	31.9	16.9	19.9	1.4	8.1
	F	6.8	14.4	30.6	18.4	21.1	1.7	6.9
Dec. 20	M	7.3	14.2	33.2	16.7	19.1	1.5	7.9
	F	6.1	13.2	32.1	17.6	20.2	1.7	9.0
Jan. 25, 1963	M	6.5	12.6	31.3	17.8	22.1	2.4	7.0
	F	6.0	15.1	29.0	16.9	22.5	2.3	8.1
Mar. 8	M	6.4	12.4	38.4	17.6	15.6	1.7	8.0
	F	7.0	12.6	39.3	16.9	16.1	1.7	8.1
Apr. 23	M	6.6	12.8	33.9	18.7	19.3	1.8	6.7
	F	6.4	13.8	33.3	16.4	20.1	1.7	8.0

[a]Main sterol components represented by peak areas have been determined as follows: X_1, C_{28} compounds; A, 22-dehydrocholesterol; B, cholesterol; C, brassicasterol or its C_{24} stereoisomer; D, 24-methylenecholesterol; X_2 and E, C_{29}-sterols.

The seasonal variations in fat content of the muscle reported here for the sea scallop may not be true of other species of scallop. Mason (1959) found no obvious seasonal variation in the composition of the muscle of *Pecten maximus* from Manx inshore waters, although the mature gonads showed a five-fold increase in fat content. On the other hand, growth rings on the shell of the Bay scallop, *Pecten irradians* indicate that spawning causes a retardation of growth in this species (Gutsell, 1930).

In this study, the variation in the composition of the sterols of the scallop does not appear to be as great as that reported by Toyama and Tanaka (1954) for the pelecypod, *Corbicula leana*. However, the compound effect of variations in the fat and sterol content creates a marked difference in the final sterol composition of the whole muscle (Fig. 3) during the pre-spawning period (August). The low sterol values at this time would indicate a transfer of these materials from the muscle to the gonad. The depletion of fats in samples taken in the late winter, a period of slow growth and presumably of fasting, was accompanied by an increase in the percentage of unsaponifiable materials and sterols in the

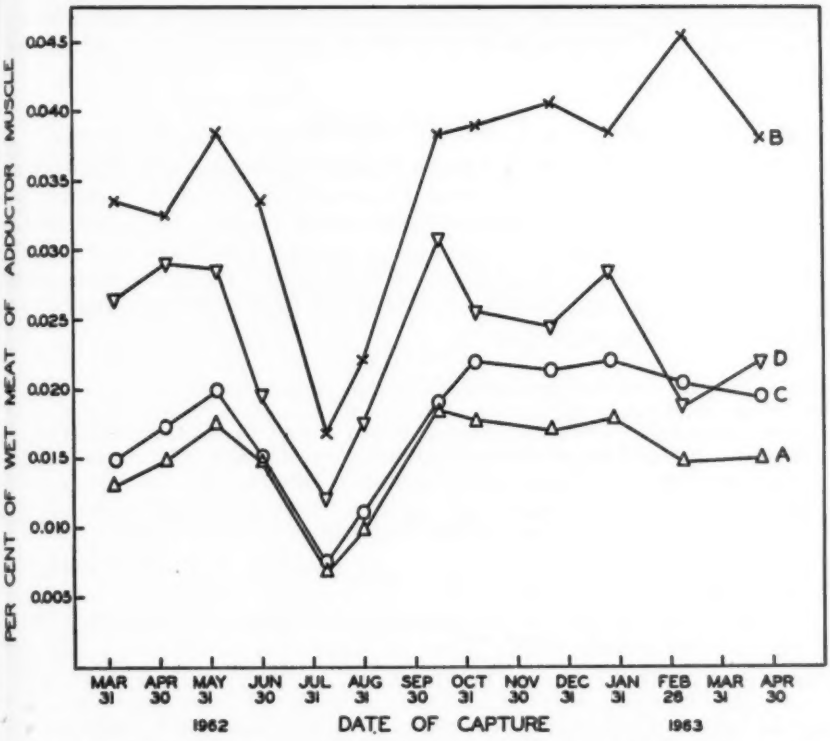


FIG. 3. Comparison of sterol composition of whole muscle of scallop during the pre-spawning period (August) and the retarded growth period (February, March). Components A, B, C, D, were identified as 22-dehydrocholesterol, cholesterol, brassicasterol, and 24-methylenecholesterol. The percentage values represent the average of values obtained for male and female scallop samples.

fats. The increase in cholesterol (component B) content per unit weight of flesh found in the March sample agrees with the results of Idler and Bitners (1958) for non-feeding migrating sockeye salmon. The changes in the cholesterol content were opposed by changes in the 24-methylenecholesterol (component D) content (Fig. 2). The explanation of the relationship between these two components may depend upon the rate of metabolism, synthesis, or conversion of these sterols, a rate determined by the environmental and biological condition of the animal. Fagerlund and Idler (1961) showed that in the clam, *Mytilus californianus*, cholesterol-4-C^{14} was converted into radioactive 24-methylenecholesterol and that at least a part of the 24-methylenecholesterol found in clams (over 50% of the total sterols) was supplied by biosynthesis within the animal.

The investigation reported here has shown that some changes in the composition of the muscle of the scallop are seasonal in nature. However, a full

explanation of the variations found in the sterol composition of marine invertebrates requires a better understanding of the metabolism and biosynthesis of sterols in the animal.

ACKNOWLEDGMENTS

The authors wish to thank Miss B. Truscott for assistance in preparation of this manuscript and Mr F. C. Read of Lunenburg Sea Products, Lunenburg, Nova Scotia, for obtaining samples of scallops each month. The advice of Dr R. G. Ackman concerning the gas chromatography procedures is gratefully acknowledged. Thanks are also due to Dr N. Bourne of the Fisheries Research Board of Canada Biological Station, St. Andrews, N.B., for information regarding the life history of the sea scallop.

REFERENCES

BERGMANN, W. 1940. The splitting of digitonides. *J. Biol. Chem.*, **132**: 471–472.

1962. Sterols: Their structure and distribution, pp. 103–162. *In* Comparative Biochemistry, Volume III, Part A, Academic Press, New York.

DAMBERGS, N. 1959. Extractives of fish muscle. 2. Solvent–water ratio in extraction of fat and water solubles. *J. Fish. Res. Bd. Canada*, **16**: 63–71.

FAGERLUND, U. H. M., AND D. R. IDLER. 1956. Marine sterols. II. 24-methylenecholesterol in molluscs. *J. Org. Chem.*, **21**: 372–373.

1960. Marine sterols. VI. Sterol biosynthesis in molluscs and echinoderms. *Canadian J. Biochem. Physiol.*, **38**: 997–1002.

1961. Marine sterols. IX. Biosynthesis of 24-methylenecholesterol in clams. *Ibid.*, **39**: 1347–1355.

GLOVER, M., J. GLOVER AND R. A. MORTON. 1952. Provitamin D_3 in tissues and the conversion of cholesterol to 7-dehydrocholesterol *in vivo*. *Biochem. J.*, **51**: 1–9.

GUTSELL, J. S. 1930. Natural history of the bay scallop. *Bull. U.S. Bur. Fish.*, **46**: 569–632.

IDLER, D. R., AND I. BITNERS. 1958. Biochemical studies on sockeye salmon during spawning migration. II. Cholesterol, fat, protein, and water in the flesh of standard fish. *Canadian J. Biochem. Physiol.*, **36**: 793–798.

MASON, J. 1959. The food value of the scallop, *Pecten maximus* (L.) from Manx inshore waters. *Rep. Mar. Biol. Sta. Port Erin*, **71**: 47–52.

POSGAY, J. A., AND K. D. NORMAN. 1958. An observation on the spawning of the sea scallop, *Placopecten magellanicus* (Gmelin), on Georges Bank. *Limnol. Oceanog.*, **3**: 478.

STEVENSON, J. A., AND L. M. DICKIE. 1954. Annual growth rings and rate of growth of the giant scallop, *Placopecten magellanicus* (Gmelin) in the Digby area of the Bay of Fundy. *J. Fish. Res. Bd. Canada*, **11**: 660–671.

TAMURA, T., T. WAINAI, B. TRUSCOTT AND D. R. IDLER. 1964. (In press.) Isolation of 22-dehydrocholesterol from scallop. *Canadian J. Biochem.*

TOYAMA, Y., AND T. TANAKA. 1954. Sterols and other unsaponifiable substances in the lipids of shell fishes, Crustacea and Echinoderms. XIV. Unsaponifiable components other than corbisterol in the lipid of *Corbicula*. *Bull. Chem. Soc. Japan*, **27**: 264–267.

WAINAI, T., T. TAMURA, B. TRUSCOTT AND D. R. IDLER. 1964. The application of gas chromatography to the identification of the sterols of scallop. *J. Fish. Res. Bd. Canada.* (Submitted for publication.)

Thermal Resistance of Pike (*Esox lucius* L.), Muskellunge (*E. masquinongy* Mitchill), and their F_1 Hybrid[1]

By D. P. Scott[2]

Fisheries Research Board of Canada
Biological Station, London, Ont.

ABSTRACT

Comparison of thermal resistances of pike, muskellunge, and their F_1 hybrid indicates close similarity between the two species. There appears to be some hybrid vigour in that the hybrids tend to be more resistant to thermal stress at the average acclimation and test temperatures encountered in the experiments. The greatest difference between the hybrids and parents occurred at the lowest test temperatures. Differences between the parent species were apparent only in their response to acclimation temperature, the slope of the curve of resistance time on acclimation temperature being much steeper for muskellunge than that for pike.

INTRODUCTION

The northern pike (*Esox lucius* L.) and the muskellunge (*E. masquinongy* Mitchill) are generally considered to be quite closely related species. One of the criteria sometimes used to test the closeness of such specific relationships has been the similarity of the thermal resistance of the species. As part of a general program of fish genetics being carried out at the Laboratory for Experimental Limnology, Maple, Ontario, lethal temperature relationships of various species are being studied, including those of the above-mentioned species and their F_1 hybrid.

Fry *et al.* (1946) have described the various ways in which thermal tolerance and resistance may be determined. In this study, only the upper region of thermal resistance was determined. A restricted number of specimens made the determination of the upper incipient lethal temperatures or the lower region of thermal resistance impractical.

MATERIALS AND METHODS

Adult pike and muskellunge were first obtained in the spring of 1962 and stripped at the laboratory. Attempts were made to rear the young of both species and the reciprocal hybrids. Both species and the hybrids require live fish for food and are highly cannibalistic. Few animals were reared beyond 5.0 cm because of these difficulties. Enough were available, however, to run preliminary trials, and these showed that it is almost impossible to obtain thermal

[1]Received for publication January 6, 1964.

[2]Seconded to the Great Lakes Institute, University of Toronto, under whose auspices the work was performed in the Department of Zoology.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

resistance regressions for fish acclimated to temperatures lower than 25°C. The specimens acclimated to 22.5°C and lower either died almost instantly when placed in the lethal baths, or else survived indefinitely. Therefore, the experiment was repeated in the spring of 1963 and adequate numbers of pure pike and F_1 hybrids (muskellunge female × pike male) were bred in the laboratory. Since all the adult male muskellunge available proved to be sterile, muskellunge young were procured from the Deer Lake Hatchery, Ontario Department of Lands and Forests. All three groups were reared to a minimum length of 5.0 cm and subdivided into groups acclimated to 25.0, 27.5, and 30.0°C.

The lethal trials were carried out in running-water aquaria maintained at various temperatures between 32.0 and 35.5°C. Water temperatures within each tank did not vary more than ±0.01°C throughout the trials. Fry *et al.* (1946) showed that the logarithm of time to death plotted against test temperature resulted in a linear relationship; therefore, times to death were recorded on a logarithmic basis in this study. The base unit used was one day, and the time scale set up as follows:

$$t_0 = 1.0 = 14.4 \text{ min}$$
$$t_1 = 1.1 = 18.1 \text{ min}$$
$$t_2 = 1.2 = 22.8 \text{ min, etc.}$$

The use of a preset log time scale ensures equal precision of measurement of the variate throughout, whereas exact recording of death time results in greater relative precision as time progresses. For the statistical procedures, the midpoint of each interval was used as the log time to death of all the animals which died within that interval. Finally, those specimens which died within the first 14.4 min were left out of the calculations, since it was obvious from their appearance that death was the result of shock, i.e. sudden temperature *change* rather than the more usual effect of the temperature itself. Observations were carried out until either all animals were dead in a particular bath or it became obvious that no more would die from temperature alone. Only one group would feed at the elevated test temperatures, namely, the hybrid group acclimated to 25.0°C being tested at 32.0°C. All others refused food, and most of the long-term deaths at the lower test temperatures seemed to be due to starvation, as indicated by their extremely emaciated appearance at death.

Statistical treatment of the data was by analysis of multivariate covariance, as outlined by Snedecor (1946) and Dixon and Massey (1957), adapted somewhat by the author. This method was adopted in order to put the effect of acclimation temperature on a quantitative basis. There being only three acclimation temperatures, arithmetic values of these were used in the analyses. On a more extended range with some other species, some transformation of the variate might be necessary.

RESULTS

The results of the analyses are presented in Tables I and II. Figure 1 shows the mean log time to death versus test temperature for each genetic group and acclimation temperature.

TABLE I. Table of statistics for between-groups comparisons of variations in thermal resistance of northern pike (P), muskellunge (M), and their F_1 hybrid (H). Probability levels: * denotes $0.05 \geqq P > 0.01$; ** denotes $P \leqq 0.01$. Variates are: $X_1 = \log_{10}$ (resistance time in thousandths of days); X_2 = acclimation temperature in °C; X_3 = lethal bath temperature in °C. Standard statistical symbols after Snedecor (1946).

Statistic	Symbol	Group			Pair totals			Grand total
		Pike	Hybrid	Muskellunge	P vs H	P vs M	H vs M	
Number of specimens	n	130	189	160	319	290	349	479
Means of variates	$\overline{X}_1$	2.012	2.022	1.967	2.018	1.987	1.997	2.001
	$\overline{X}_2$	27.46	27.63	27.89	27.56	27.70	27.75	27.67
	$\overline{X}_3$	33.98	34.10	34.08	34.05	34.04	34.09	34.06
Sums of squares of deviations from means	Sx_1^2	13.1853	24.7014	22.7444	37.8939	36.0778	47.7087	60.9171
	Sx_2^2	549.81	721.69	642.34	1273.75	1207.35	1371.81	1929.54
	Sx_3^2	85.46	99.29	108.27	185.70	194.37	207.58	294.05
Simple correlation coefficients	r_{12}	+0.077	+0.245**	+0.225**	+0.179	+0.155	+0.229	+0.189
	r_{13}	−0.808**	−0.760**	−0.701**	−0.771	−0.743	−0.727	−0.744
	r_{23}	+0.489**	+0.397**	+0.498**	+0.440	+0.496	+0.445	+0.460
Multiple correlation coefficients	$R_{1.23}$	0.973**	0.966**	0.964**	0.963	0.957	0.953	0.954
Standard partial regression coefficients	$b'_{12.3}$	+0.621**	+0.649**	+0.763**	+0.643	+0.689	+0.694	+0.673
	$b'_{13.2}$	−1.113**	−1.018**	−1.081**	−1.054	−1.087	−1.034	−1.053
Standard errors of regression coefficients	$s_{b'}$	0.0234	0.0207	0.0245				
Standard errors of differences between regression coefficients and degrees of freedom[a]	$s_{d'}$				0.0314	0.0339	0.0321	
	d.f.				285.41	282.96	323.30	
Group variances	s^2	0.00550	0.00890	0.01027				

Equations:
For pike: $X_1 = 14.183 + 0.096X_2 - 0.436X_3 : X_1 = 1.989$ at Q
For hybrid: $X_1 = 16.029 + 0.120X_2 - 0.508X_3 : X_1 = 2.047$ at Q
For musky: $X_1 = 14.848 + 0.143X_2 - 0.495X_3 : X_1 = 1.945$ at Q
where Q = adjusted mean X_2 and X_3 for all three groups.

[a]Calculations according to Dixon and Massey (1957).

TABLE II. Various statistical contrasts between pairs of groups and the total sample in adjusted group means, regression coefficients and variances. Symbols as in Table I. Tests used are: analysis of covariance for adjusted group means; variance ratio for pairs comparison of variance; Bartlett's test for homogeneity of variance, and Student's "*t*" test modified for comparison of standard partial regression coefficients. Analysis of covariance was used to test for homogeneity of regression coefficient of X_1 on the *resultant* of X_2 and X_3 in total sample. Degrees of freedom in parentheses.

Contrast	Test for equality of			
	Adjusted group means	$b'_{12.3}$	$b'_{13.2}$	Variance
Total	$F = 21.27^{**}$ (2,472)	$F = 29.69^{**}$ (4,470)		$\chi^2 = 13.70^{**}$ (2)
P vs H	$F = 13.74^{**}$ (1,315)	$t = 0.892$ (285.41)	$t = 3.025^{**}$	$F = 1.618^{**}$ (186,125)
P vs M	$F = 28.30^{**}$ (1,286)	$t = 4.189^{**}$ (282.96)	$t = 0.944$	$F = 1.867^{**}$ (157,127)
H vs M	$F = 92.53^{**}$ (1,345)	$t = 3.551^{**}$ (323.30)	$t = 1.963^{*}$	$F = 1.154$ (157,186)

It can be seen from the Tables that considerable differences exist between the groups. These differences are relatively small in magnitude, but owing to the extremely small variances associated with the multiple regressions, such differences are highly significant. At the average acclimation and test temperatures, the three groups are highly different, the hybrid being most resistant, the muskellunge least so, and the pike intermediate. When the relationship between resistance time and the *resultant* of acclimation and test temperatures is examined, these also show highly significant differences. Here, however, a breakdown of the resultants into the partial slopes shows that significant differences really exist in only two coefficients: (1) the slope of resistance time on acclimation temperature of muskellunge is different from the other two, and (2) the slope of resistance time on test temperature of the hybrids is different from the others. In addition, the variance of the pike relationship is significantly less than the others. Thus, each of the three groups has one particular part of its thermal resistance relationship which is different from the others.

It should be noted that there is a definite break in the linearity of the regressions at about log time = 2.75 (approximately 800 min). From here on, the regression curves become more horizontal, and, from all appearances, subsequent deaths appear to be caused by starvation. These extended death periods were not included in the analyses.

DISCUSSION

From the results presented above, a number of points is immediately obvious. Despite the highly significant differences shown, the general patterns of thermal resistance are quite similar. The very high multiple correlation coefficients show that there is little variability not accounted for by the combined effects of acclimation and test temperatures.

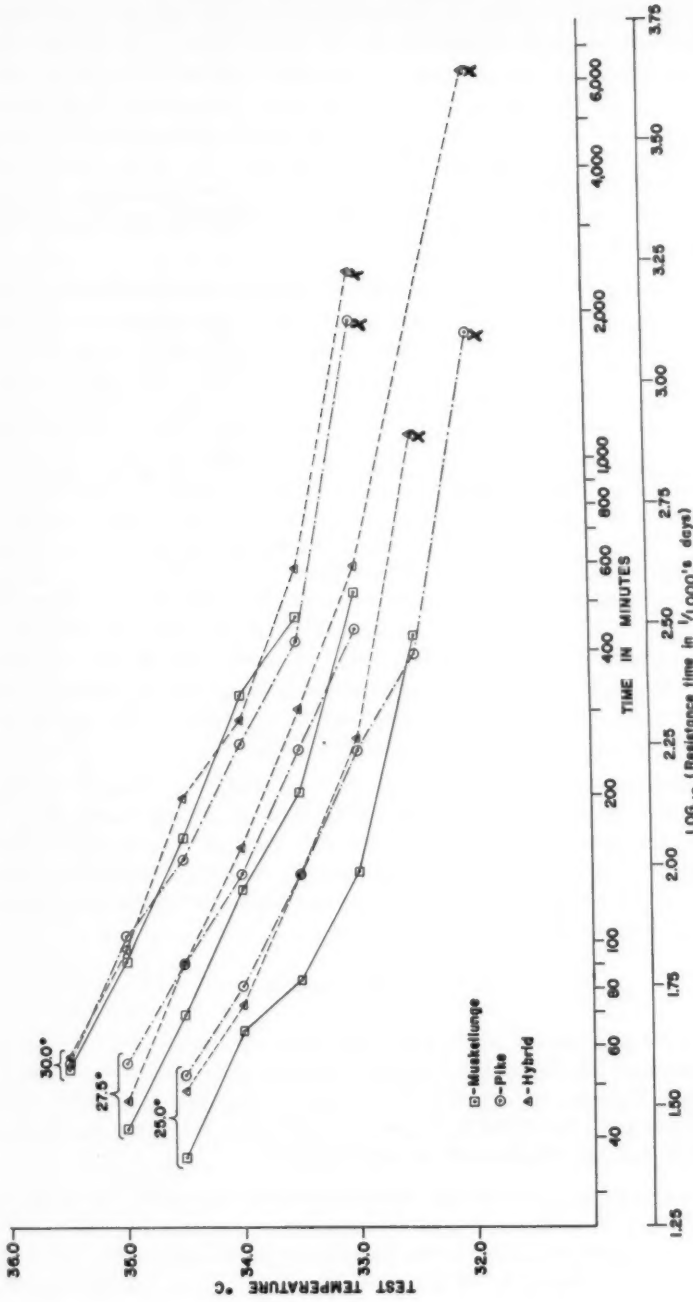


FIG. 1. Time (mean) to death at various lethal and acclimation temperatures for pike, muskellunge and F_1 hybrid. X signifies group not included in analyses.

The differences shown to exist are characteristic of each group, but are not precisely what one might expect on a purely genetic basis. The hybrid is intermediate between its parents only in variance and response to acclimation temperature. Its test temperature response is represented by a shallower curve than either parent, and from Fig. 1, the greatest difference appears to take place at the lower test temperatures. It would appear that some sort of hybrid vigour might be involved here. It is obvious that the patterns of response to acclimation temperature and test temperature resistance are not simple, i.e. more than one gene locus is involved.

The question of why longer trial periods should be associated with deviations from linearity arises when all the specimens died in a particular sample, apparently from thermal effects. It has been postulated that some acclimation may take place in the lethal baths during a particular test. Brett (1946) showed that there was a lag in response of goldfish to a change in temperature. It might be supposed that if such a lag exists in the esocids, the deviations from linearity of the regressions would appear only at the low test temperatures where resistance times are sufficiently long to permit some acclimation. This is indicated in the present data, as shown in Fig. 1. Hart (1947) showed that the resistance time versus test temperature regressions for different acclimation temperatures were not parallel for some species, and further that the incipient lethal was reached at an earlier time at the lower acclimations. When these facts are taken with Brett's data and the present study, it would indicate that there is some sort of dosage–response curve involved; that is, the lag may be shorter at the lower acclimation temperatures because the temperature difference between acclimation and test temperature is greater. The rate of acclimation may also be enhanced by the greater difference.

In summary, there appears to be close similarity in thermal resistance relationships of pike and muskellunge, while their F_1 hybrid shows some distinct differences from either parent. This may indicate hybrid vigour in that the differences are to the benefit of the hybrid. Some acclimation appears to take place in the lethal baths, as shown by moderate deviations from linearity at the longer test periods.

ACKNOWLEDGMENTS

This work was carried out in the Laboratory for Experimental Limnology which is operated jointly by the Research Division of the Ontario Department of Lands and Forests, and by the Department of Zoology, University of Toronto. Grants from the Ontario Research Foundation and National Research Council were used for supplies and technical services.

Sincere thanks are given to the following persons who made the study possible: Dr F. E. J. Fry, University of Toronto, who suggested the study; Mr R. Jones, formerly chief technician at the Laboratory for Experimental Limnology, Maple, who reared the stocks of fish; and Mr A. V. Tyler, graduate student,

who assisted in making the observations often at very inconvenient hours of the day and night. Thanks also are due to members of the Fish Culture Branch, Ontario Department of Lands and Forests, for their co-operation in providing specimens.

REFERENCES

BRETT, J. R. 1946. Rate of gain of heat-tolerance in goldfish (*Carassius auratus*). *Univ. Toronto Stud., Biol. Ser.*, No. 52; *Pub. Ontario Fish. Res. Lab.*, No. 64, pp. 9–28.

DIXON, WILFRED J., AND FRANK J. MASSEY, JR. 1957. Introduction to statistical analysis. McGraw-Hill Book Co., Inc., 2nd Ed., 488 pp.

FRY, F. E. J., J. S. HART, AND K. F. WALKER. 1946. Lethal temperature relations for a sample of young speckled trout, *Salvelinus fontinalis*. *Univ. Toronto Stud., Biol. Ser.*, No. 54; *Pub. Ontario Fish. Res. Lab.*, No. 66, 35 pp.

HART, J. S. 1947. Lethal temperature relations of certain fish of the Toronto region. *Trans. Royal Soc. Canada*, **41**(3): 57–71.

SNEDECOR, GEORGE W. 1946. Statistical methods. Iowa State College Press, 4th edition, 483 pp.

Preliminary Results of Studies on Growth and Mortality of Pacific Cod (*Gadus macrocephalus*) in Hecate Strait, British Columbia[1]

By K. S. Ketchen

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Preliminary results of tagging suggest that the Brody-Bertalanffy growth coefficient, K, of cod in northern Hecate Strait is 0.27 and the asymptotic length, L_∞, is 94.0 cm. Life span is relatively short and the fishery appears to be dependent on fish which have completed 3 and 4 years of growth. Estimates of present day instantaneous total mortality rate, based on average length of fish in the catch, range from 1.05 to 1.53 (65–78% on an annual basis) depending on fishing area and length at full recruitment. Mortality rates of 0.83 and 0.99, computed from primitive length composition, may indicate the order of magnitude of the instantaneous natural mortality rate (56 and 63% expressed as an annual rate).

INTRODUCTION

This is the second of two papers dealing with the problem of obtaining accurate measures of the growth and mortality of Pacific cod or "grey cod" in Canadian waters. It is preliminary to the extent that, because of still unresolved difficulties in age determination which prevent a simple attack on the problem through age structure, much depends on a "patch-work" of information based on observation of changes in length composition and on rather sparse returns from tagging. The difficulties which are encountered in age determination and in the results of tagging are in large measure attributable to the fact that in Canadian waters the cod is close to the southern limit of its range. There, apparently in response to a high temperature environment, growth seems to proceed unchecked throughout at least the initial years and is accompanied by an exceptionally high rate of natural mortality. The preliminary results from Hecate Strait, nevertheless, appear to be valuable in indicating the order of magnitude of the parameters of growth and mortality and hence set the stage for more painstaking investigation.

Previous studies (Ketchen, 1961) have shown that cod of Hecate Strait (53° to 54° N lat) inhabit slightly colder water (6–7°C) than those of southern British Columbia (7–9°C). In the Strait of Georgia (ca. 49° N lat), it has been demonstrated from tagging results that the cod has a substantially higher initial growth rate than in much colder regions of the North Pacific such as Bering Sea and Sea of Okhotsk; it matures at an earlier age and has a relatively short life span. Total mortality rate, though possibly overestimated at 70–

[1]Received for publication May 20, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

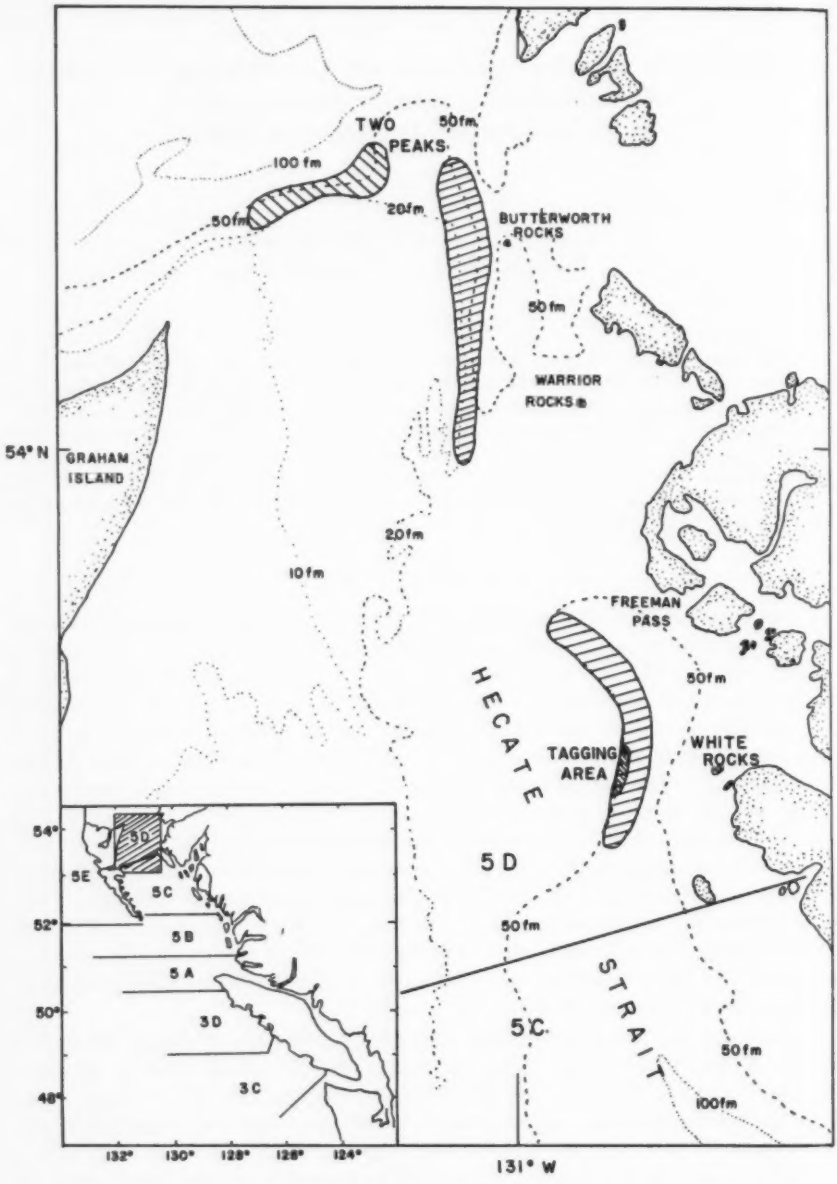


FIG. 1. Northern Hecate Strait, British Columbia, showing the main trawling grounds for Pacific cod.

80% per annum nevertheless appears to be relatively high, a major share of which appears to be due to natural causes. It remained to be determined whether these observations applied to other waters of British Columbia, and for this reason Hecate Strait was selected for study since it represents the most northerly (and coldest) segment of the British Columbia coast.

BACKGROUND

Hecate Strait Stocks of Cod

Knowledge of the distribution of cod in Hecate Strait may be gained from information on the trawl fishery in that region. During late autumn and winter, cod fishing takes place in the southern part of Statistical Area 5D, primarily on the ground adjacent to Freeman Pass and White Rocks (Fig. 1). This region, henceforth referred to as the White Rocks ground, appears to be the main site of spawning. In the succeeding spring months most of the cod catches occur 20–40 miles to the northward along the Butterworth–Warrior "edge" and on the Two Peaks ground at the northern extremity of the Hecate Strait bank. The summer fishery, though of lesser importance than that early in the year, is focussed on the Two Peaks ground and also in the region of the Horseshoe

Table I. Known production of Pacific cod from the southern (Area 5C) and northern (Area 5D) subdivisions of Hecate Strait (round weights in millions of pounds)[a]; and calculated average catch per unit of effort in Area 5D[b].

Year	Area 5C			Area 5D			Area 5D average C/E (*lb*)
	Canada	U.S.	Total	Canada	U.S.	Total	
1945	0.016	...	...	0.162	...	...	...
1946	0.050	...	...	0.847	...	...	...
1947	0.011	...	...	0.179	...	...	...
1948	0.019	...	...	0.206	...	...	...
1949	0.007	...	...	0.496	...	...	...
1950	0	...	...	0.863	...	...	...
1951	0.404	...	...	2.651	...	...	1,960
1952	0.031	...	...	1.724	...	...	1,000
1953	0.001	...	...	0.331	...	...	690
1954	0.032	...	...	1.736	...	...	940
1955	0.115	0.570	0.685	1.205	2.928	4.133	765
1956	0.806	0.132	0.938	0.964	1.359	2.323	585
1957	0.338	0.072	0.410	1.973	2.731	4.704	885
1958	2.096	0.704	2.800	4.316	4.353	8.669	1,560
1959	0.600	1.150	1.750	4.153	5.395	9.548	1,105
1960	0.673	0.213	0.886	3.084	1.232	4.316	775
1961	0.070	0.003	0.073	2.658	0.831	3.489	610
1962	0.361	0.001	0.362	3.186	0.176	3.362	530

[a]Canadian records from Nanaimo Biological Station Statistical Circular Series, Vol. 1–12; 1956–60 totals from 14th Annual Report of the Pacific Marine Fisheries Commission, with remainder from manuscript material. Totals exclude small amounts landed by Canadian vessels for minkfood.

[b]Basis for calculation of catch per unit effort described in text footnote no. 2.

ground in lower central Hecate Strait (Area 5C). Seasonal movements in relation to depth and water temperature have already been described (Ketchen, 1961, p. 524).

In February 1960 and again in February 1961, tagging of cod was conducted aboard the Fisheries Research Board of Canada trawler *A. P. Knight* on the southern part of the White Rocks ground. In the first year 1214 fish were tagged and released, followed by 1033 in the second year. Preliminary results reported by Thomson (1961) indicated that dispersion from the tagging area was predominantly to the northward within Area 5D. To February 1963, a total of 527 (23.3% of the combined numbers released) had been returned. Of 481, for which place of recapture was reported, 402 were retrieved in the area of tagging, mainly within 2 months of release and to a lesser extent in the succeeding autumn and winter. Of the remaining 79 recaptures made outside the tagging area, 75 were reported from Butterworth–Warrior ground and Two Peaks ground, and only four were reported outside Area 5D (vicinity of the Horseshoe ground in

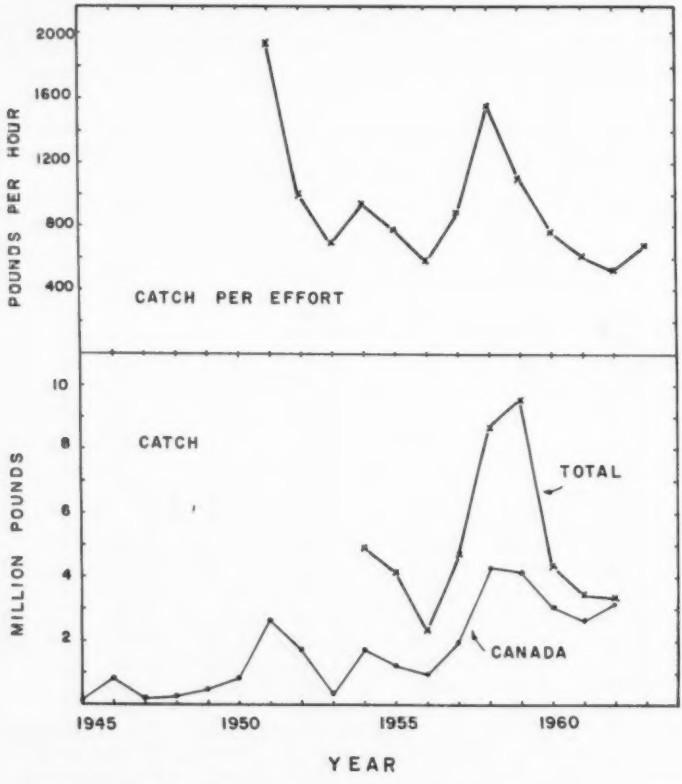


FIG. 2. Pacific cod catches and estimated catch per unit of effort from grounds in northern Hecate Strait (Area 5D).

TABLE II. Monthly landings of Pacific cod from Area 5D (northern Hecate Strait) by Canadian and United States trawlers (weights in millions of pounds)*.

Month	Year							Average per cent of annual catch
	1956	1957	1958	1959	1960	1961	1962	
Jan.	0.062	0.335	0.525	0.991	0.515	0.629	0.474	10.0
Feb.	0.256	0.428	1.078	2.876	0.585	0.723	0.808	17.3
Mar.	0.809	1.518	2.531	1.560	0.810	0.628	0.489	23.4
Apr.	0.441	1.081	1.688	0.771	0.340	0.495	0.175	13.8
May	0.421	0.222	0.386	0.111	0.206	0.216	0.080	6.0
June	0.090	–	0.045	0.023	0.114	0.073	0.033	1.5
July	0.110	0.185	0.577	1.023	0.333	0.291	0.673	8.9
Aug.	0.017	0.002	0.304	0.592	0.448	0.059	0.179	4.0
Sept.	0.033	–	0.025	0.321	0.551	0.132	0.177	3.9
Oct.	–	0.117	0.265	0.552	0.225	0.093	0.060	3.0
Nov.	0.046	0.578	0.315	0.474	0.109	0.059	0.103	4.3
Dec.	0.050	0.241	0.933	0.257	0.083	0.091	0.111	4.1
Total:	2.335	4.707	8.672	9.551	4.319	3.489	3.362	

*Source: 14th Annual Report of the Pacific Marine Fisheries Commission (1956–60); manuscript (1961–62).

Area 5C). For present purposes it is reasonable to assume that the stock (or stocks) of cod in Area 5D are more or less separate from those in southern Hecate Strait and other areas of the British Columbia coast.

HISTORY OF PRODUCTION IN AREA 5D

The cod fishery of British Columbia is conducted exclusively by otter-trawlers. Complete records which include catches by United States vessels are available only from 1955 onwards, though detailed statistics on the Canadian fishery began in 1945 — early in the development of the modern-day trawl fishery in Hecate Strait. Available information on the two statistical subdivisions of Hecate Strait is given in Table I and records specifically for Area 5D are graphed in Fig. 2. Substantial fluctuations in production have occurred during the past decade. Likewise considerable instability in relative abundance is suggested by the data on catch per unit of effort[2].

As shown in Table II, most of the catch in Area 5D (over 60% on the average) is taken in the period January through April. January and February landings are largely from the White Rocks ground, while those of March and April come from grounds farther to the north. Frequently, substantial quantities of cod are taken on the Two Peaks ground in July, but by late autumn the fishery is once again concentrated on the White Rocks ground.

[2]Calculations of catch per unit of effort are based on the performance of Canadian double-gear trawlers in the 25–49 gross tonnage class. To reduce, if not eliminate, the effect of fisheries for other species and hence arrive at an estimate of "effective" fishing effort on cod, the analysis was restricted to the catch and effort of those vessels whose landings contained at least 25% by weight of cod and which fished on the White Rocks ground during the months of January through March and on the Warrior–Two Peaks ground during March and April.

SIZE COMPOSITION OF CATCHES ON THE WHITE ROCKS GROUND

The length–frequency distributions of cod encountered on the White Rocks ground in February 1960 and 1961 by the research vessel *A. P. Knight* are shown in Fig. 3. Catches were made with a conventional "western box trawl"[3] having a cod-end constructed of "Drumlene" (a synthetic fibre) with an internal, stretched-mesh size of about $3\frac{3}{4}$ inches (9.5 cm). In the 1960 catches three size groups were evident, with modal lengths around 26, 43, and 55 cm. The first of these groups was absent from the 1961 catches.

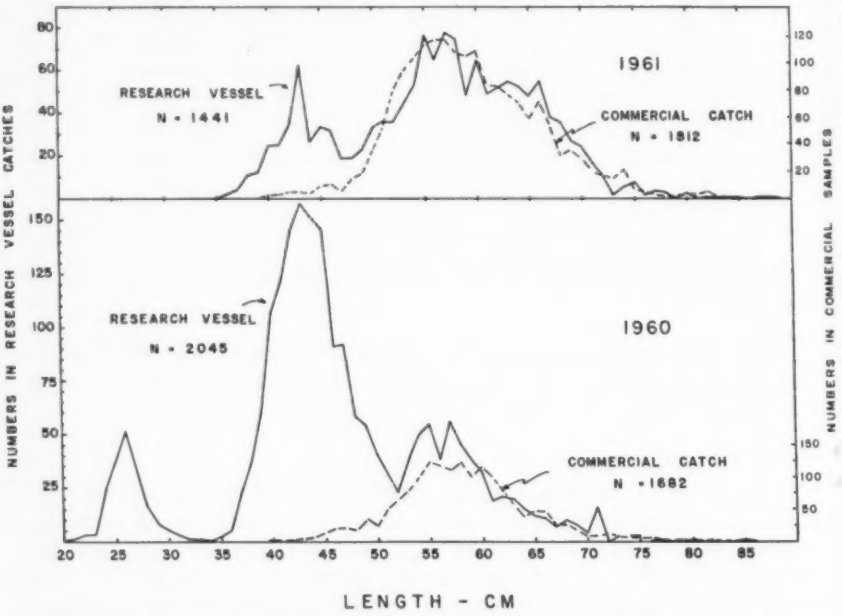


FIG. 3. Length–frequency distributions of cod caught by the research vessel *A. P. Knight* on the White Rocks ground in February 1960 and 1961, as compared with length–frequency distributions in commercial landings.

Superimposed on the length distributions obtained by the research vessel are the average distributions in samples collected from commercial landings made at the same time of year from the same general fishing area. Exact duplication could not be achieved because the research vessel was not always fishing in the same locality or at the same depth as the commercial vessels. However, the data suggest that the fishery is selective for the larger sizes of cod, most of those less than 50 cm in length being rejected at sea[4]. From time to time some

[3]A four-sided trawl with a 90-ft, rope-wrapped groundline.

[4]Figure 3, particularly the 1960 data, may not reflect the true proportion of rejected fish. Commercial vessels would tend to avoid localities and depths where unmarketable sizes predominate. During the course of the research vessel's stay on the White Rocks ground considerable heterogeneity was noted in the size composition of the day-to-day catches. It is well known to fishermen that individual shoals of cod vary in size composition.

vessels land unselected or partially selected catches from which the smaller individuals are saved for animal food (mink food market). Larger individuals, when landed at Vancouver and other south coast ports, are usually dressed (gutted) and are used in the fresh and frozen fillet trade, while those landed at Prince Rupert (round or dressed) may be processed as frozen fillets or stored for later sale as halibut bait.

ESTIMATION OF GROWTH

Growth Indicated by Length–Frequencies

Although information on the growth of juvenile cod in Hecate Strait is only fragmentary, it is sufficient to establish that the first two modal groups contained in the research vessel catches of 1960 (Fig. 3) represent fish which have completed 1 and 2 years of growth, respectively. On June 14, 1954, a sample of 140 young cod taken in several hauls with a small-meshed (1–1¼-inch) trawl (at depths of 14–16 fathoms) had an average length of 9.1 cm (range: 6.3–11.5 cm). These data are shown as item A in Fig. 4[5]. On June 16, 1952, another sample of young cod was taken on the Horseshoe ground in Area 5C. These fish had an average length of 32.9 cm (range: 22–42 cm) and are shown as item B in Fig. 4, at assumed age of 16 months. By means of probit analysis, it was found that the normal curves calculated from the length–frequency distributions of the first two modal groups in Fig. 3 (1960) had mean lengths of 26.0 and 43.5 cm. These appear as items C and D in Fig. 4 at assumed ages of 12 and 24 months, respectively.

The smoothness of the curve connecting means A to D suggests that the assumptions regarding age are reasonably valid. Thus the curve is a useful first approximation of growth to the end of the second year. Clearly, much more sampling will be required to test its representativeness throughout northern Hecate Strait and its year-to-year consistency[6].

Growth Indicated by Tag Returns

Tagging in 1960 and 1961 was restricted to cod of lengths greater than 36 cm. During the 11th to 13th month after release only 33 fish were recaptured (from the combined taggings) for which reliable information was provided on length at recapture. Even fewer could be identified as to sex in view of the general tendency of fishermen to gut their fish before landing. The average time which the 33 tagged fish had been at liberty was 362 days, or, for practical purposes, one year even ($T = 1$).

[5]For present purposes it is presumed that mid February marks the beginning of the "cod year" in Hecate Strait, for this is approximately the mid-point in the spawning season as observed on the White Rocks ground. On this basis the age of the small cod taken in the June 1954 sample is estimated as approximately 5 months.

Slight difference in average length from that given by Ketchen (1961) results from inclusion of more data.

[6]Some question also remains concerning the effect of mesh selection on the estimated length at completion of age I (Fig. 4, item C). Although no direct evidence is available, it is possible that the length distribution for that age lies partly within the selection range of the mesh size used by the research vessel. Thus the mean length for the age-I fish may be overestimated.

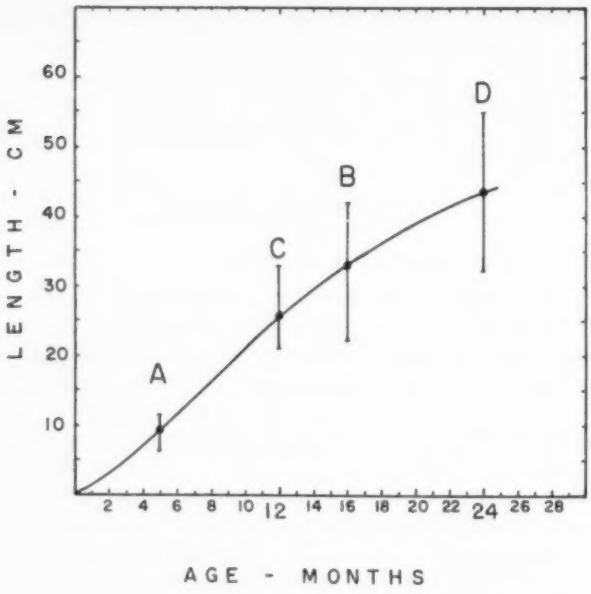


FIG. 4. Approximation of growth of cod in Hecate Strait during the first 2 years of life. (See text for details.)

To determine growth rate, use is made of the modified Walford-type relationship between length at time of tagging (l_t) and length at a specified time after tagging (l_{t+T}). The increment of growth $l_{t+T} - l_t$ is plotted against l_t as in Fig. 5. This is a graphical expression of the modified Brody-Bertalanffy equation:

$$l_{t+T} - l_t = L_\infty (1 - e^{-KT}) + l_t (e^{-KT} - 1) \quad (1)$$

where K is the growth coefficient, L_∞ is the asymptotic length and T is the time interval (for other forms of the growth equation see Ricker, 1958, p. 192).

In Fig. 5 there appear to be two groups of returns, those represented by the lines A and B (fitted by least squares). Half of those in the former group were identified as to sex and all were males. However, two verified males also appeared in the B group.

A similar grouping emerges if recoveries during the 8th to 10th month period after release are treated in like manner (Fig. 6). The presence of verified males and females in both groups casts doubt on the possibility that the two groupings (A and B) reflect a sex difference in growth. In the absence of better data, it seems likely that there are fast and slow growing components in the White Rocks aggregation which are independent of any difference which may exist in the growth by sex.

For present purposes we shall assume that the weighted line C (in both Fig. 5 and 6) reflects growth of the stock as a whole. The slope of line C in

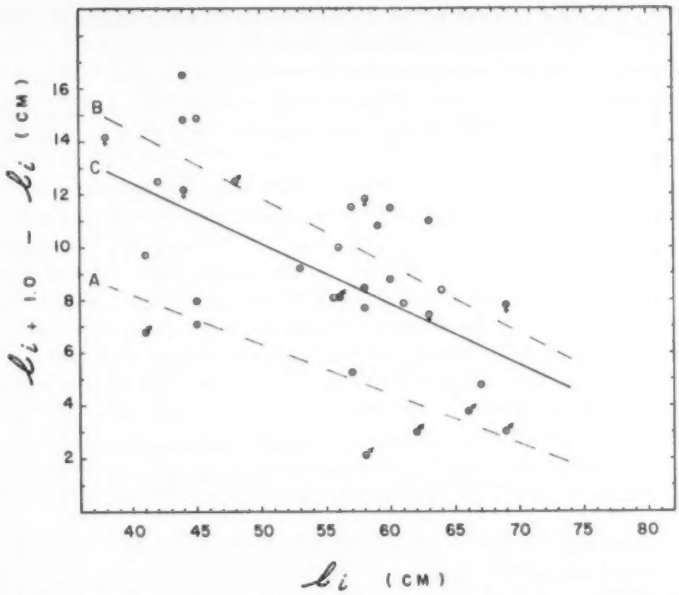


FIG. 5. A modified Walford graph showing the relation between length of cod at time of tagging (l_i) and the increment of growth $l_{i+T} - l_i$, where T (time out) equals 1.0 years. (Measurements in centimetres.)

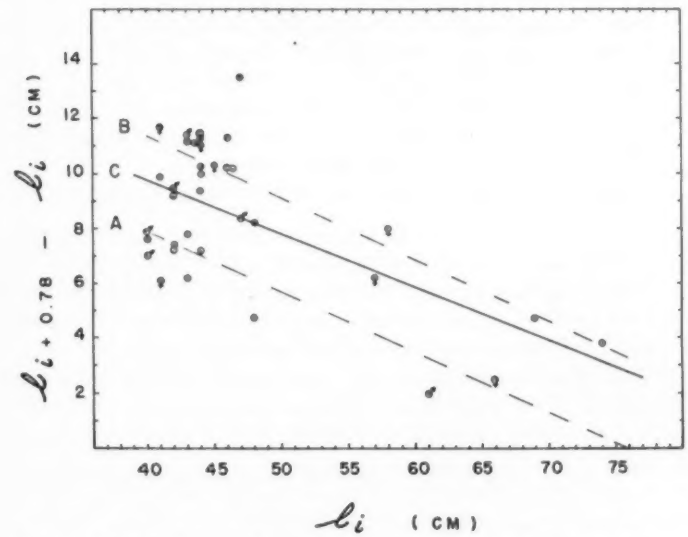


FIG. 6. Relation between l_i and $l_{i+T} - l_i$ where $T = 0.78$ year. (Measurements in centimetres.)

Fig. 5 ($e^{-KT} - 1$ from equation (1)) is found to be –0.232. Since $T = 1$, it follows that $K = 0.27$ and $L_\infty = 94.0$ cm. In Fig. 6 the slope of line C is –0.195, whence, given $T = 0.78$, we find that $K = 0.28$ and $L_\infty = 90.3$ cm. These values, though acceptably close to those obtained from Fig. 5, will be excluded from subsequent calculations, as they are based on fewer returns from the larger sizes of fish tagged.

From the preceding section, it is estimated that the average length of cod at completion of the second year of growth is 43.5 cm. Substituting $K = 0.27$ and $L_\infty = 94.0$ cm in equation (1) and using $l_t = 43.5$ cm as a starting point, we may estimate the average lengths at succeeding ages. These calculated lengths, together with the observed lengths for ages I and II are plotted in Fig. 7 from Table III. Also shown in the figure is the curve calculated for the Strait of Georgia, using the lowest of several possible values of K (from Ketchen, 1961), namely, 0.56 with corresponding L_∞ of 75.0 cm. As in the construction of the Hecate Strait growth curve, observed lengths were used for ages I and II and lengths for succeeding ages were calculated from equation (1).

As noted previously there is some question regarding the reliability of the observed length at age I in the Hecate Strait data. If we assume that the

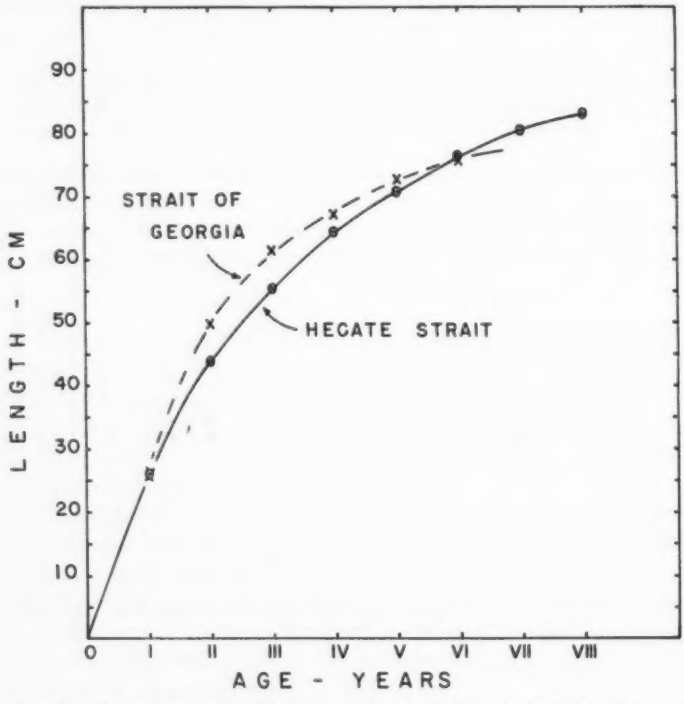


FIG. 7. Comparison of calculated growth curves for cod of northern Hecate Strait and the Strait of Georgia.

TABLE III. Calculated average length at each age, average weight at each age and estimated instantaneous growth rate (g).

Age (completed years)	Average length (cm)	Average weight[a] (g)	Average weight[a] (lb)	Log_e (wt)	Instantaneous growth rate (g)
I	26.0	190	0.42	5.26	1.59
II	43.5	950	2.09	6.85	0.74
III	55.2	1,980	4.37	7.59	0.47
IV	64.2	3,160	6.97	8.06	0.32
V	71.1	4,350	9.60	8.38	0.22
VI	76.4	5,430	11.98	8.60	0.16
VII	80.5	6,380	14.06	8.76	0.12
VIII	83.6	7,180	15.84	8.88	

[a]From the length–weight formula $W = .00788\ L^{3.100}$.

Brody-Bertalanffy equation applies over the full range of ages then from the intercept $L_\infty\ (1-e^{-KT})$ we obtain a calculated value of 22.3 cm for length at age I, which is lower than the observed. It remains to be determined which of these is closest to the true value.

The direction but perhaps not the magnitude of the difference between the estimates of K and L_∞ for the Strait of Georgia and northern Hecate Strait is as expected. Beverton and Holt (1960, p. 167) point out that within populations of the same species living in different areas food and temperature account for most of the variation found. Food supply modifies the asymptotic length while environmental temperature affects both K and L_∞. With increase in water temperature K increases while L_∞ decreases.

LENGTH COMPOSITION OF COMMERCIAL LANDINGS

Sampling of the commercial landings of cod from northern Hecate Strait began in a small way in 1950. At that time and until about 1955, most of the catches were made in the months of March to May on grounds from the Warrior-Butterworth edge to the Two Peaks. During the period 1955–63 the pattern of fishing (at least by Canadian vessels) changed somewhat, with emphasis shifting more to the White Rocks area. On the average about 55% of the annual catch now comes from that area (mainly in January to March) with the remainder from the original fishing grounds to the north (March and April).

Available information on the length composition of cod landings from the two main fishing areas in northern Hecate Strait is illustrated in Fig. 8. Samples from the White Rocks ground apply to the period January–March, while those from the Warrior-Two Peaks region apply to March–April (or in a few cases March–May for want of sufficient data covering the shorter period).

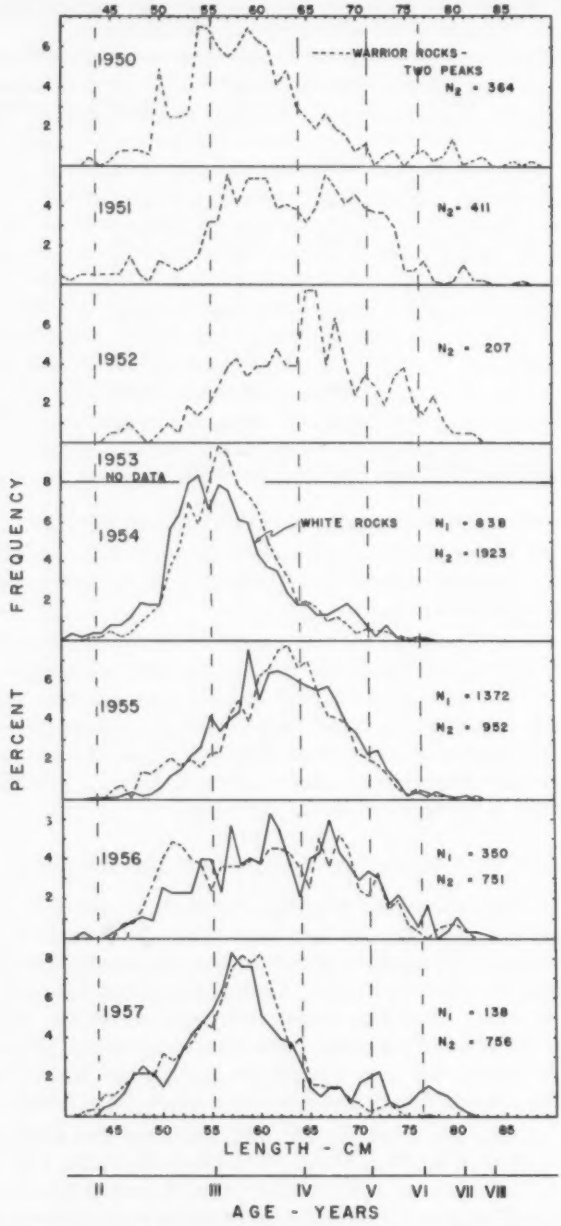
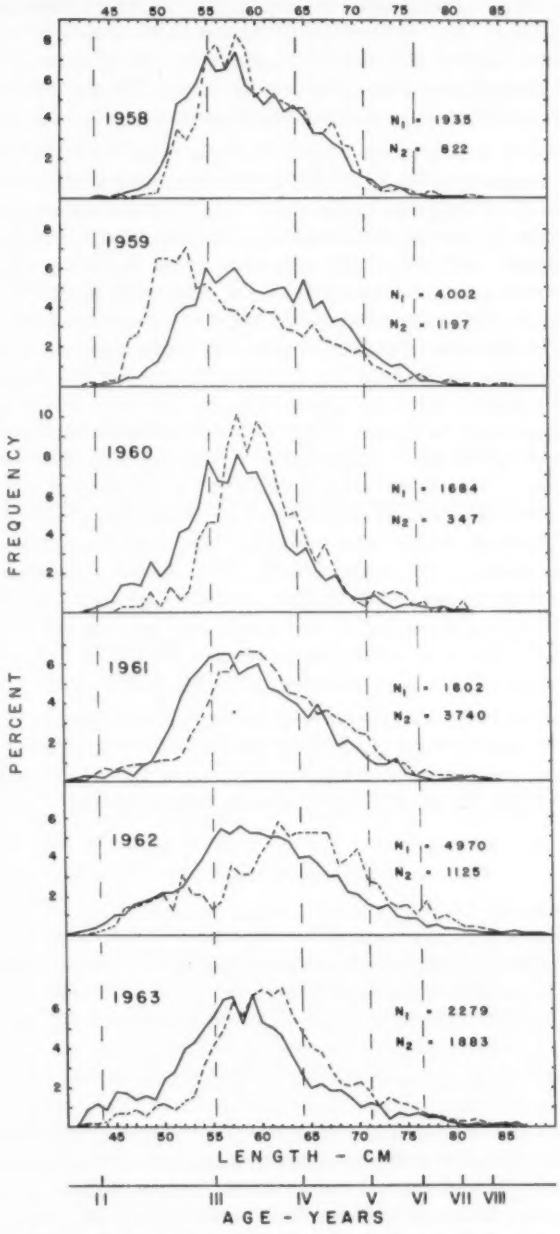


FIG. 8. Length–frequency distributions of cod in commercial landings from the tw



the tw grounds in northern Hecate Strait compared with calculated length at each age.

Superimposed on the length–frequency distributions is the age–length key derived from Table III. A general conclusion to be drawn from these data is that the foodfish fishery is dependent mainly on cod of ages III and IV, and that there is negligible contribution of fish of age VI and over. On matters of detail, however, there is a question of interpretation.

If we assume that the age–length index is valid, not only for the period to which the tagging results apply (1961–63) but also for all of the other years of observation, then explanation must be found for the apparent disparity between the domes of the length–frequencies and the calculated mean lengths for age. For example, in most of the years the dome ostensibly representing fish of age III lies somewhat to the right of the calculated length for that age (in the case of White Rocks samples) or squarely between the calculated lengths for age III and IV (Warrior–Two Peaks samples). There are two possible causes of this discrepancy: (1) Because of selection for size by the fishery (a process which in all likelihood varies in degree from year to year for economic as well as other reasons) only the larger 3-year-olds are retained for market. In other words, not until cod reach a length of 55–60 cm are they free from the effects of culling at sea. This is partially borne out by the data of Fig. 3. (2) Cod may segregate by size (and/or sex) once they leave the White Rocks ground, the larger individuals being more prone to move northward to the Warrior–Two Peaks grounds in the early spring. This factor plus effects of culling, with a few notable exceptions (e.g. data of 1956 and 1959) would explain the presence of cod which according to the age–length key are not easily classed as either age III or IV, being either the larger age III fish or the smaller age IV, with combined abundance after selection, in excess of any single older age group.

On the other hand the disparity may reflect weakness in the age–length key, in that it fails to take account of year-to-year variability in growth, or differing growth rates by sex or by components of the northern Hecate Strait stock which support the fishery on the several fishing grounds.

MORTALITY RATES

Beverton and Holt (1956, p. 69) have demonstrated that, given a measure of the growth rate in terms of the Brody-Bertalanffy growth equation and information on the average length of fish in the catch, it is possible to obtain an approximation of total mortality rate. The relationship is expressed as

$$(F+M) = \frac{K(L_\infty - \bar{l})}{\bar{l} - l'} \qquad (2)$$

where $(F+M)$ is the instantaneous rate of total mortality, $\bar{l}$ is the average length of fish in the catch that are as large or larger than the first fully recruited length, l'. This method was used to estimate the mortality rate of cod in the Strait of Georgia, where, as in Hecate Strait, direct information on age structure is lacking (Ketchen, 1961).

Already mentioned is the lack of precise information on the process of selection for size by the trawlers operating in Hecate Strait. However, it seems likely that the first fully recruited length (l') or "fully retained" length is somewhere between 55 and 60 cm. These extremes will be used to set limits on the estimates of total mortality rate, as based on the values of $K = 0.27$ and $L_\infty = 94.0$ cm (from page 1060).

To overcome at least partially the effects of fluctuating recruitment, the length–frequencies shown in Fig. 8 have been averaged by groups of years. Estimates of $(F+M)$, based on these grouped data for each of the major fishing areas of northern Hecate Strait, are given in Table IV. Depending on the choice of l', the estimates for the White Rocks ground range from 1.12 to 1.37 (67 to 75%, expressed on an annual basis). Estimates for the Warrior–Two Peaks grounds for the same groups of years (1954–58; 1959–63) range from about 1.05 to 1.53 (or 65 to 78% on an annual basis).

TABLE IV. Estimates of instantaneous total mortality rate $(F + M)$ from length–frequencies grouped by years for each of the major fishing grounds in Area 5D and for each of two assumed values of length at full recruitment.

Length at full recruitment (l')	White Rocks ground		Warrior–Two Peaks ground	
	55 cm	60 cm	55 cm	60 cm
1950–52	–	–	0.83	0.99
1954–58	1.12	1.29	1.23	1.53
1959–63	1.19	1.37	1.05	1.26

Where it is assumed that $l' = 60$ cm, the estimates are comparable to those obtained from the Strait of Georgia. In that region, l' was estimated as 60 cm and values of $(F+M)$ ranged from 1.27 to 1.62 depending on the choice of several possible values of K and L_∞ (Ketchen, 1961, p. 544).

The estimates of $(F+M)$ calculated from the 1950–52 data for the Warrior–Two Peaks grounds, namely 0.83 and 0.99 (corresponding annual rates 56 and 63%), provide a clue to the possible magnitude of M (instantaneous natural mortality rate), since they apply to a period when the Hecate Strait cod fishery was in its infancy. However, the length–frequencies for those early years exhibited considerable instability possibly because of substantial variation in recruitment and/or inadequate sampling. Thus cautious interpretation is necessary. Nevertheless, it is worth noting that, if the present-day true value of $(F+M)$ is around 1.25 and if M is within the range 0.83–0.99, then by subtraction the instantaneous fishing mortality rate (F) is within the range 0.26–0.42 (23–34% on an annual basis). Such values are not inconsistent with those calculated for other important species of groundfish which are exploited along the British Columbia coast. If on the other hand we assume that the relatively

low value of $(F+M)$ from the 1950–52 data, emerged by chance alone, then we are left with the interesting speculation that natural mortality rate is density dependent.

Whatever the cause, it is apparent that natural mortality rate is high in comparison with most other demersal fishes and this has an obvious implication from the standpoint of fishery management, namely, that greater yield from a given recruitment could be achieved by increased fishing and by reduction of the minimum market size (for further discussion see Ketchen, 1961; Forrester and Ketchen, 1963).

RESEARCH NEEDS

Lack of a satisfactory (objective) method of age determination of cod in British Columbia waters is a major stumbling block to accurate measurement of growth and mortality parameters. While further efforts should be made to resolve this difficulty, much could be gained in the meantime by a greatly intensified program of tagging. Large-scale taggings in various regions of Hecate Strait and at various times of the year are needed not only to establish more clearly the affinities of cod on the several fishing banks but also to overcome the high rate of tag loss due to natural mortality and other factors. In support of such effort increased publicity on an international scale and increased rewards to fishermen should improve the quality of information on tag recoveries.

It is of special importance not only to confirm the apparently high rate of natural mortality but also to determine the extent and cause of its variability. It may eventually be possible to establish a relationship between fishing effort and total mortality rate which would provide an estimate of natural mortality rate. Failing this, reliance must be placed on the results of tagging which in turn depend on assessment of tagging mortality and other losses (shedding and non-reporting).

Extensive sampling at sea in the presence of commercial operations is required to establish more clearly the extent and variability of the practice of culling for size.

Before reliance can be placed on the Beverton and Holt method of estimating total mortality rate from the average size of fish in the catch, it is essential to determine whether the Brody-Bertalanffy growth equation provides an adequate description of the growth of Pacific cod. Of equal importance is knowledge of whether or not the natural and fishing mortality components can be treated as constants beyond the age of full recruitment. Without these kinds of information it is impossible to measure the direction and magnitude of bias in the present estimates of total mortality rate.

SUMMARY

1. From results of preliminary tagging conducted on cod in northern Hecate Strait in 1960 and 1961, the growth coefficient, K, is estimated as 0.27 with a corresponding asymptotic length, L_∞, of 94.0 cm. Further tagging is required

to determine whether these estimates are representative of the stock as a whole. As they stand, they differ from those estimated for cod inhabiting more southerly (warmer) waters of the Strait of Georgia (lowest value of $K = 0.56$; $L_\infty = 75.0$ cm).

2. On the basis of the preliminary age–length key it is concluded that the commercial cod fishery of Hecate Strait is dependent primarily on fish of ages III and IV (completed years). Except in cases where vessels land part of their catches for animal food, age I and II cod are rejected at sea. Apparently few cod live beyond the age of VI or VII.

3. Instantaneous total mortality rates ($F+M$) based on average size of fish in the catch and on the estimates of K and L_∞ range from 1.05 to 1.53 (65–78% expressed as an annual rate) assuming that size at full recruitment is within the limits of 55–60 cm.

4. ($F+M$) estimates of 0.83 and 0.99 (or 56 and 63% on an annual basis) apply to a period early in the development of the Hecate Strait cod fishery and hence may be indicative of the order of magnitude of the instantaneous natural mortality rate.

5. In the absence of a satisfactory method of age determination, there is need for more extensive tagging in Hecate Strait, improvement of information accompanying tag returns, field tests to determine more accurately the effects of selection for size by the commercial fishery, and tests of tagging mortality and losses from other causes.

ACKNOWLEDGMENTS

The writer wishes to acknowledge with thanks the contribution of Mr J. A. Thomson who carried out the Hecate Strait tagging projects and processed the data therefrom. Dr P. A. Larkin, Director of the Biological Station, and members of the groundfish investigation provided helpful criticisms of the manuscript.

REFERENCES

BEVERTON, R. J., AND S. J. Holt. 1956. A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. *Rapp. Cons. Expl. Mer*, **140**(1)9: 67–83.

1960. A review of the life spans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Ciba Foundation Colloquia on Ageing, **5**: 142–180. J. and A. Churchill, London.

FORRESTER, C. R., AND K. S. KETCHEN. 1963. Review of the Strait of Georgia trawl fishery. *Bull. Fish. Res. Bd. Canada*, No. 139, 81 pp.

KETCHEN, K. S. 1961. Observations on the ecology of the Pacific cod (*Gadus macrocephalus*) in Canadian waters. *J. Fish. Res. Bd. Canada*, **18**(4): 513–558.

RICKER, W. E. 1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Bd. Canada*, No. 119, 300 pp.

THOMSON, J. A. 1961. Preliminary results of grey cod tagging in Hecate Strait, in 1960 and 1961. *Fish. Res. Bd. Canada, Nanaimo Station Circular* (*Statistical Series*), No. 62, 8 pp.

Some Characteristics of Nitinat Lake, An Inlet on Vancouver Island, British Columbia[1]

By T. G. Northcote, Mildred S. Wilson[2] and D. R. Hurn[3]

Fish and Game Branch of the British Columbia Department of Recreation and Conservation and the Institute of Fisheries of the University of British Columbia, Vancouver, B.C.

ABSTRACT

The morphometry, temperature, salinity, and oxygen characteristics are described for an inlet on the southwestern coast of Vancouver Island. Although the inlet is over 200 m deep, only the upper 20–30 m (about ¼ of its total volume) appears to be oxygenated. There are marked changes, both vertically and horizontally, in salinity of near-surface water. All components of the biota observed are either marine, brackish or euryhaline forms.

INTRODUCTION

The observation that Nitinat Lake contained organisms of marine origin was made by one of the authors (D. R. Hurn) several years ago. Unaware of investigations being conducted on Powell Lake, British Columbia, by the Institute of Oceanography at the University of British Columbia (Williams *et al.*, 1961), we decided to conduct brief surveys of Nitinat Lake to record the extent to which it was occupied by saline water and marine organisms. Some data from these surveys have already been published (Pickard, 1963) but are included here for convenience.

METHODS

A Furuno F-701 200 Kc/s recording echo-sounder was used to make cross-sections of the inlet at points shown in Fig. 1. A thermistor thermometer (Yellow Springs Instrument Co., Model 44TB) was used to obtain temperature profiles while conductivity was measured with a Model RB2-3341 Solu Bridge. Subsurface water samples were obtained with a Kemmerer bottle for salinity determinations (silver nitrate titration with no correction for H_2S or unusual ionic balance) and for dissolved oxygen analysis (unmodified Winkler technique). Plankton collections were taken with a standard Wisconsin plankton net fitted with No. 10 nylon mesh. The bottom fauna was sampled with a 15-cm Ekman dredge.

[1]Received for publication February 14, 1964.

[2]Present address: Arctic Health Research Center, Anchorage, Alaska. Financial support from the National Science Foundation of the United States is acknowledged (Grant G-21643 to the Smithsonian Institution).

[3]Present address: Dept. of Recreation and Conservation, Nanaimo, B.C.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

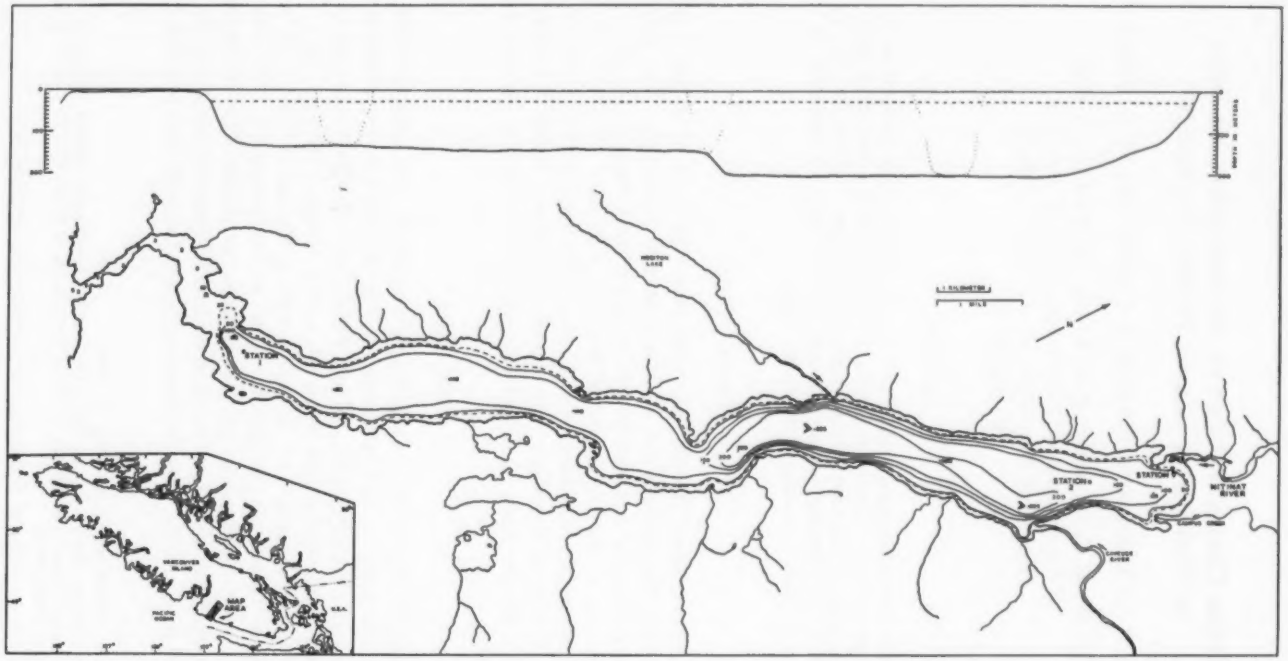


FIG. 1. Longitudinal profile and depth contours in meters of Nitinat Lake on Vancouver Island, British Columbia. Dotted lines show three approximate cross sections; probable vertical and horizontal extent of deoxygenated water mass shown below and within broken lines.

GEOLOGICAL AND MORPHOMETRIC FEATURES

Geology

Nitinat Lake (Fig. 1) on the southwestern coast of Vancouver Island lies in a transverse valley which was greatly deepened by glacial scour so that its bottom is considerably below sea level almost to its mouth. Clapp (1912) describes the transverse valley as follows: "It is now occupied by a lake – Nitinat lake – whose surface is only a few feet above low tide, so that at high tide the salt water rushes into it through a narrow rock gate."

Although rocks along the central portion of the inlet are batholithic granodiorites and those at its mouth are diorites, much of the shoreline is composed of crystalline limestones known as the Nitinat formation (Clapp, 1912). Only at the northeastern end of the inlet and along Nitinat River do metamorphosed volcanics occur.

Morphometry

The inlet, lying in a northeast–southwest oriented transverse valley, is 23 km in length, 1.2 km in mean breadth with a surface area of 27.6 km^2. Its length to width ratio of 19:1 is close to the average ratio of 20:1 given by Gilmartin (1962) for 33 typical transverse fjords in British Columbia. The maximum depth of the inlet is slightly in excess of 200 m. Values over 200 m were only recorded by the sounder at two cross-sections (Fig. 1) and in both cases the depth must have been somewhat greater than 205 m. The approximate volume of the inlet calculated from contours shown is 2750×10^6 m^3.

The inlet in longitudinal section (Fig. 1) is characterized by two, quite flat floor levels, the deeper in the northeastern half lying at about 200 m, that in the southwestern portion gradually slopes upward from 150 m to 130 m before rising rapidly to the sill at the mouth of the inlet. Depths given in Fig. 1 along the length of the narrow mouth of the inlet indicate maximum depths at each cross-section. Nitinat Lake is joined to the open Pacific Ocean by a narrow tidal passage nearly 3 km in length whose maximum depth ranges between 2 and 5 m at lowest normal tides. At high tides the sill would be about 6 to 9 m deep. Away from its head and mouth, the inlet has sharply sloping sides and a relatively flat bottom in cross-section. Only at the region of rise between the two floor levels was the inlet V-shaped rather than U-shaped in cross section (Fig. 1).

A slight tidal change in water level is evident even at the head of the inlet.

Nitinat River, the major tributary of the inlet, drains an area over 400 km^2, much of which has been heavily logged off. The river is subject to marked seasonal variation in discharge. Observations made by the Department of Fisheries of Canada (personal communication, W. J. Schouwenburg) indicate the minimal discharge in 1958 to be less than 0.7 m^3/sec whereas the maximal discharge was about a thousand times greater. On June 15, 1961, when the salinity and other measurements described later were obtained, discharge of the Nitinat River was estimated to be between 1.5 and 2 m^3/sec. The runoff patterns of the

Nitinat River and Caycuse River, a somewhat smaller tributary, have a mid-summer minimum and winter maximum, typical of most lower level coastal rivers. The inlet would probably fall into the direct-runoff inlet category distinguished by Pickard (1961).

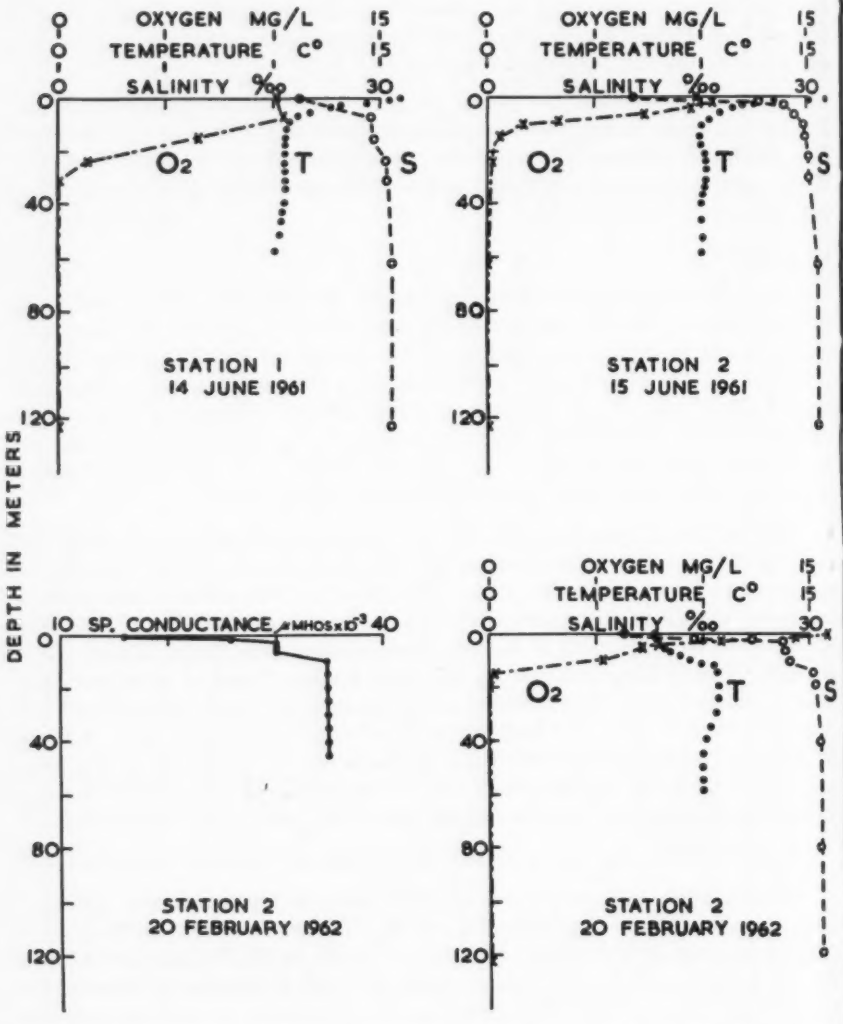


FIG. 2. Physical and chemical conditions at two stations on Nitinat Lake, British Columbia

PHYSICAL-CHEMICAL FEATURES

Temperature–Salinity Profiles

Vertical profiles of temperature and salinity were recorded at a station near the mouth of Nitinat Lake in midsummer and at a station at its head both in midsummer and midwinter (Fig. 2). At Station 2 near the head of the inlet, surface salinities of less than 10‰ were not recorded. However, river discharge was low during both sampling dates. Data from 1959 (Fig. 3) show that the salinity near the surface may fall well below 10‰, especially in the upper half of the inlet. A sharp halocline occurred in the upper 10 m, with nearly maximum salinity of 30‰ or more being reached by a depth of 20 m. On the basis of its salinity characteristics Nitinat would be a Group A.2 inlet with a Type 2 vertical salinity profile (Pickard, 1961).

In summer the temperature profile simulates a mirror image of the Type 2 salinity profile, with a sharp thermocline in the upper 10 m. No deep water temperature measurements were made; at 60 m values close to 10°C were recorded for both stations in summer and at Station 2 in winter.

Longitudinal Changes in Near-surface Salinity

Some additional information was available from the Moore-Whittington Lumber Company on changes in near-surface salinity along the length of Nitinat Lake in 1959, prior to our investigations (Fig. 3). In the January series little

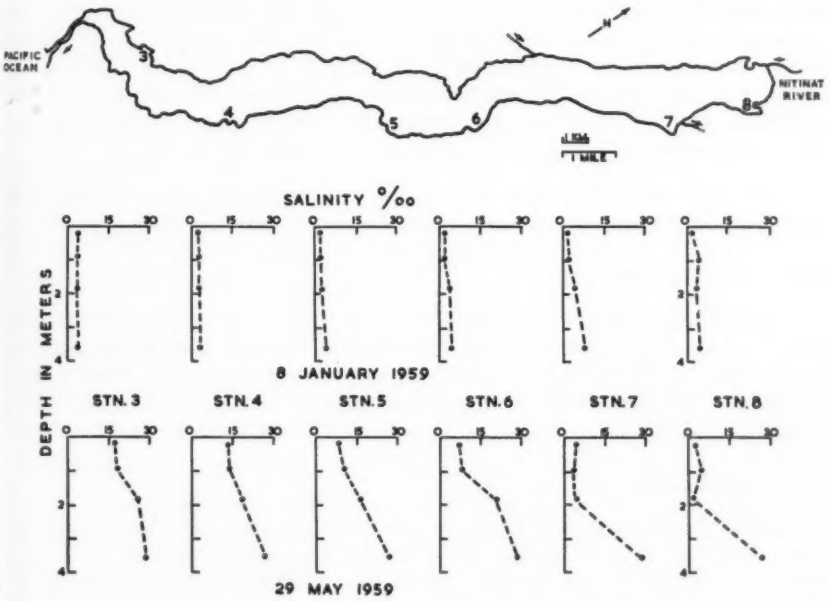


FIG. 3. Winter and late spring near-surface salinity profiles along the length of Nitinat Lake British Columbia (from data of Moore-Whittington Lumber Company).

change was evident in surface salinity between the mouth and head of the inlet. Furthermore there was only a slight increase in salinity with depth (to 4 m). A large inflow of fresh water from tributaries could account for the wide distribution of low salinity water at this time, however no flow records are available. Conditions were markedly different in the May series. Then a distinct increase in surface salinity occurred between the head and mouth of the inlet, coupled with a sharp increase in salinity between 0 and 4 m. This latter increase was greatest at the head and least at the mouth (Fig. 3).

Conductivity

A continuous vertical profile of specific conductivity was made in winter at Station 2 (Fig. 2). There was a rapid rise in conductivity in the uppermost 3 m with a sharp step in the profile between 3 and 7 m, depicting in more detail the change evident in the salinity profile. No change in conductivity was noted between 10 and 45 m, the deepest reading possible with the solubridge used.

Dissolved Oxygen

One of the most spectacular features of Nitinat Lake is extensive and extreme depletion of oxygen in its deeper water. In midsummer, zero values were recorded at all levels below 30 m at both Station 1 and 2 (Fig. 2). Similar conditions existed at Station 2 in midwinter, suggesting that the depletion may well be a permanent feature of the inlet. Stratification appears to be less sharp at Station 1 compared to Station 2, possibly resulting from periodic mixing with oxygenated saline water introduced over the sill at high tides. If the 30-m level represents a characteristic and more or less permanent level of complete oxygen depletion in Nitinat Lake, then at least 73% of its total volume would be deoxygenated. The horizontal and vertical extent of this layer is indicated in Fig. 1.

The high supersaturations near the surface at Station 2 in February 1962 were probably caused by the dense bloom of phytoplankton present then.

Hydrogen Sulphide

Presence of hydrogen sulphide was noted in all water samples taken below a depth of 30 m in the inlet. At Station 2 on June 15, 1961, no H_2S was apparent at 20 m but it was present in samples from 30 m. Samples from the same station on February 20, 1962, exhibited no odour of H_2S at 15 m but a strong H_2S odour at 20 m.

Light Penetration

Secchi disk readings of 7.5 m were recorded at Station 1 and 2 in June 1961. Little difference in light penetration would be expected between the head and mouth of the inlet at that time because of the low and clear discharge from the Nitinat and other tributary rivers. These readings are in the same range as those recorded by Pickard (1961) for inlets with small rivers or streams.

BIOLOGICAL FEATURES

PHYTOPLANKTON

Samples taken from vertical hauls (0–60 m) at Station 1 and 2 in summer and from surface tows at Station 2 and 9 in winter were examined by Dr Janet Stein, Department of Biology and Botany, University of British Columbia and Miss G. A. Heron and Mr L. A. Hobson, Department of Oceanography, University of Washington. Results of their identifications are summarized in Table I. No strictly freshwater forms were noted, many species probably being euryhaline.

TABLE I. Phytoplankton from Nitinat Lake samples taken on June 14–15, 1961 and February 20, 1962.

Genus — species	Occurrence*			
	June 1961		February 1962	
	Station 1	Station 2	Station 2	Station 9
Ceratium macroceros (Ehrenberg)	++	++		+
Chaetoceros affinis Lauder		+	+	
Chaetoceros curvisetus Cleve		+		
Chaetoceros danicus Cleve	++	++		
Chaetoceros debilis Cleve	+			
Chaetoceros decipiens Cleve	+		+	+
Chaetoceros didymus Ehrenberg		+		
Chaetoceros subsecundus Hustedt			+	+
Ditylum brightwellii (West)		+		
Melosira numuloides (Dillwyn)		+		
Nitzsedia seriata Cleve			+	
Rhizosolenia hebetata (Bailey)			+	+
Sceletonema costatum (Grenville)			+	
Stephanopyscis nipponica Gran & Yendo			+	
Tabellaria fenestrata (Lyngb.) Ktz.		+		
Thalassionema nitzschioides Grunow		+		
Thalassiosira decipiens Grunow			++	++
Thalassiosira pacifica Gran & Angst			++	

*Although no attempt was made to examine samples quantitatively, species occurring in very large numbers are designated by ++; presence is indicated by +.

Zooplankton

Pelagic zooplankton was sampled at Station 1 and 2 in June 1961 and at Station 2 and 9 in February 1962. The cladocerans and copepods identified from the samples are listed in Table II. Samples were examined only for species composition and developmental stages; estimates of the numbers of abundant species and counts of the specimens of the rarer species were made. Small jellyfish, fragments of siphonophores, and ctenophores noted in some samples were not identified.

Sampling at Station 1 was more restricted than at Station 2 and may account for the smaller number of species recorded in Table I. Possibly, however, seasonal differences related to life cycles, salinity or physical conditions conversely affected occurrence or collection of some species in summer and winter.

Samples from Station 2 consisted of surface tows and series of stage hauls from 10–60 m. All of the 13 species listed in Table II were recorded in the upper water mass (0–15 m) where the abundant species of Table II occurred in their greatest numbers. Of these, about 5000 specimens of all stages of *Eurytemora affinis* were collected in February, far surpassing any other species. Only two species, *Paracalanus parvus* and *Oncaea subtilis*, were noted in stage hauls restricted to the deeper, largely deoxygenated water (15–60 m) at this station in June. In February, these two species also occurred in hauls to 60 m with *E. affinis*, *Acartia longiremis* and one specimen of *Corycaeus affinis*. A surface tow made at Station 9 near the mouth of Nitinat River contained comparatively few individuals but a large number of species. Interestingly, this sample lacked specimens of freshwater genera such as *Daphnia* and *Diaptomus* that might be carried into the inlet by streams. There are, however, no large lakes draining into the Nitinat River.

The crustaceans listed in Table II are neritic species previously reported from inshore-offshore waters of the British Columbian or neighbouring coasts. Most are broadly distributed in marine and brackish waters in temperate regions of the northern hemisphere and several are common constituents of plankton along the northern coast of North America, where combinations of some of the same species found in Nitinat Lake have been reported (Johnson, 1961).

The copepods belong to a diverse group of families whose genera appear repeatedly in accounts of plankton of coastal water, estuaries, maritime brackish lakes and so-called inland seas. Many have a wide range of salinity and temperature tolerance although only one, *Eurytemora affinis*, is known to establish populations in fresh waters. Conceivably, this species occurs in fresh waters of British Columbia but there are no known records. Indeed, the only Pacific coast occurrence presently listed in a geographic index of continental calanoid copepods currently being compiled is in Lake Merced, San Francisco, California (unpublished data, M. S. Wilson). Freshwater records are commoner for the North American Atlantic and Gulf of Mexico coastal regions, where the farthest inland penetration has been about 300–450 miles (186–279 km) from the nearest coast, into Lake Erie (Engel, 1962) and Lake Avalon, Carlsbad, New Mexico (unpublished data, M. S. Wilson).

Nitinat Lake appears to present a remarkable opportunity for both challenging and rewarding study of zooplankton, particularly in the copepods. To be meaningful, observations should be made over an annual period for several consecutive years, it being of primary importance to determine whether all or some species have established permanent populations in the inlet or if occurrence is of a temporal nature dependent upon tides and weather. It is probably valid speculation that *Eurytemora affinis* is a permanent resident because of its euryhaline characteristics; its common and often persistent occurrence in estuaries; the collection in Nitinat Lake of large numbers of a reproducing population as indicated by the presence of many females carrying ovisacs with developing ova, nauplii and all developmental copepodid stages. Observations of three other species also point to reproducing populations at the time of our collections. Both sexes of *Oncaea subtilis* were found; females carried ovisacs in June; developmental copepodid stages were present and unidentified cyclopoid nauplii were probably in this species. Nauplii and early copepodid stages of *Acartia longiremis* were positively identified. All developmental stages of *Paracalanus parvus* were not found but the species occurred in all samples, sometimes in fairly abundant numbers. Another species, *Pseudocalanus elongatus*, was not collected in great numbers but some of the females carried ovisacs in February. This is either a variant of or closely related to the widely distributed *P. minutus* (Krøyer) studied by McLaren (MS, 1961) in a landlocked fjord on Baffin Island, suggesting that the Nitinat species might be adaptable to living in an enclosed body of water. (The species designation used here follows suggestions and comments of D. M. Damkaer, University of Washington, who compared Nitinat specimens with those he is currently studying from neighbouring coastal waters and to which he has applied the name *P. elongatus*, which has been treated in literature as a full species, a variant form or synonym of *P. minutus*.)

Benthonic Algae

A well-developed band of the attached brown alga, *Fucus evanescens* C. Ag., extended along the shores of the inlet from its mouth to about a mile north of Station 6 (Fig. 3). An epiphytic filamentous brown alga, *Pylaiella littoralis* (Zyngb.) Kjellm., was associated with samples of *Fucus* collected in June 1961.

Bottom Fauna

Samples were taken near the head of Nitinat Lake on July 15, 1961. At depths of 33 and 45 m, the bottom was composed of a soft black mud giving off a strong H_2S odour. No organisms were found in samples at either depth. A more compacted brown mud was present between 10 and 15 m. Samples in that region contained many small polychaete worms. These were examined by C. Berkeley at the Fisheries Research Board of Canada Biological Station, Nanaimo, but fragmentation and poor preservation prevented positive identification. They probably were spionid polychaetes belonging to the genus *Spio*. Molluscan fauna in the 10–15-m zone consisted largely of the gastropod *Nassarius mendicus* Gould although fragments of *Mytilus edulis* Linn. shell were noted.

Specimens of the crab, *Cancer gracilis* Dana, and a shrimp, *Crangon franciscorum* (Stimpson), were taken in the littoral region near the head of the inlet. A number of amphipods belonging to the typically brackish water species *Anisogrammarus convervicolus* Stimpson were collected in association with the *Fucus* zone between Station 6 and 7.

Fish

Collections of fish were obtained by gill netting and shore seining near the head of the inlet in June 1961. Juvenile Pacific herring, *Clupea pallasii* Valenciennes, and shiner seaperch, *Cymatogaster aggregata* Gibbons, were taken in gill nets set along the bottom at 5–10 m in depth while the threespine stickleback, *Gasterosteus aculeatus* Linnaeus, starry flounder, *Platichthys stellatus* (Pallas), staghorn sculpin, *Leptocottus armatus* Girard, prickly sculpin, *Cottus asper* Richardson, and Aleutian sculpin, *Cottus aleuticus* Gilbert, were captured in seine hauls around the mouth of Campus Creek. Juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum) as well as threespine stickleback, prickly and Aleutian sculpins were collected in the Nitinat River upstream from the inlet.

The Department of Fisheries of Canada record runs of several thousand coho and chinook salmon, *O. tshawytscha* (Walbaum) and greater numbers of chum salmon, *O. keta* (Walbaum) spawning in Nitinat River tributary to the inlet. Steelhead trout, *Salmo gairdnerii* Richardson, are taken frequently by anglers in this river. Spawning sockeye, *O. nerka* (Walbaum) and chum salmon are known to ascend the Hobiton River from Nitinat Lake.

In addition, spawning runs of pink salmon, *O. gorbuscha* (Walbaum) and migratory coastal cutthroat trout, *Salmo clarkii clarkii* Richardson, have been reported from the Nitinat system.

DISCUSSION

Nitinat Lake, in direct contrast to most inlets along the mainland coast of British Columbia studied by Pickard (1961), appears to be physically similar to some of the shallow-silled Norwegian fjords described by Strøm (1936). None of the British Columbia mainland inlets which have been examined shows the extreme and extensive oxygen depletion evident in all water below 30 m in Nitinat. In Vancouver Island, Saanich Inlet reaches a comparable level of depletion at depths below 100 m (Herlinveaux, 1962) and at times the deeper water in Tofino Inlet has no oxygen (Pickard, 1963). Indeed, the lake may represent an intermediate stage between an inlet whose largely deoxygenated bottom water is periodically flushed and a low-lying lake with a surface layer of fresh water and a bottom layer of stable, deoxygenated saline water such as has been described for Saelsø (Trolle, 1913), Powell Lake (Williams *et al.*, 1961), and occurs in Saginaw Lake on the Sechelt Peninsula of British Columbia (Northcote and Johnson, 1964). The present salinity of water in Nitinat Lake below 20 m approximates that of the adjacent ocean which would suggest at least sporadic exchange possibly during periods of high tide and storms.

No strictly freshwater forms were evident either in the flora or fauna of Nitinat Lake, even at the surface near the head of the inlet. Although the brown alga *Fucus* was absent from this region, many components of the fauna were typically marine or brackish forms.

A complete gradation in marine to fresh water nature has been noted in the lochs of North Uist, one of the Hebrides Islands (Murray and Pullar, 1910). One of the lochs on North Uist, Loch Oban nam Fiadh, has a lower basin affected by all ordinary tides and containing marine plants and animals but apparently some freshwater plants as well. Its upper basin is only influenced by highest tides and supports some freshwater plankters such as *Holopedium*. Loch Caravat, draining into Loch Oban nam Fiadh by a short stream, maintains a typical freshwater fauna but yet occasionally exhibits tidal changes in level.

The largely marine nature of Nitinat Lake is similar to another of the North Uist lochs, Obisary, described by Murray and Pullar (1910). This barely tidal loch opening to the sea by a shallow, narrow channel is the largest and deepest

TABLE II. Cladocera and Copepoda from Nitinat Lake samples taken on June 14–15, 1961 and February 20, 1962.

Family	Genus — species	Stage[a]	Occurrence[b]			
			June 1961		February 1962	
			Sta. 1	Sta. 2	Sta. 2	Sta. 9[c]
CLADOCERA:						
Polyphemidae	*Evadne nordmanni* Lovén	Ad, Imm	++	++++		
	Podon polyphemoides Leuckart	Ad		++++		
COPEPODA, CALANOIDA:						
Calanidae	*Calanus* sp.	CI–V		+	+	+
Paracalanidae	*Paracalanus parvus* (Claus)	CIV–VI	+++	+++	++	+
Pseudocalanidae	*Pseudocalanus elongatus* (Boeck)	CIV–VI	+		+	++
Centropagidae	*Centropages abdominalis* Sato	CV–VI				+
Temoridae	*Eurytemora affinis* (Poppe)	CI–VI, N		++++	++++	++
Acartiidae	*Acartia longiremis* (Lilljeborg)	CII–VI, N			+++	++
	Acartia clausi Giesbrecht	CVI			+	+
Tortanidae	*Tortanus discaudatus* (Thompson and A. Scott)	CVI			+	
COPEPODA, CYCLOPOIDA:						
Oncaeidae	*Oncaea subtilis* Giesbrecht	CIII–VI	+++	++++	+++	
Oithonidae	*Oithona* sp.	CVI			+	
Corycaeidae	*Corycaeus affinis* McMurrich	CVI			+	+

[a]Ad = adult; Imm = immature stages; CI–VI = copepodid stages I–VI (C VI is the adult); N – naupliar stages.

[b]Relative abundance of species indicated by + (= 2–5 specimens) to ++++ (500–5000 specimens.

[c]Surface sample taken about 200 m south of the mouth of Nitinat River.

(46 m) on North Uist. A slight temperature inversion was noted in water below 30 m which may indicate infrequent mixing of more saline bottom water. Marine mussels and crustacea occur among the vegetation, which apparently includes freshwater plants. Gurney (1931, pp. 230, 236) noted that the plankton of Loch Obisary consisted of *Evadne nordmanni*, *Acartia clausi*, *A. discaudata* and *Centropages hamatus*. The first two species also occur in Nitinat Lake while the calanoid copepod *Centropages* is represented by another species (Table II).

Absence of any true freshwater biota has been noted for Nuwuk Lake, a shallow, halocline lake on Point Barrow Peninsula, Alaska (Mohr *et al.*, 1961). In this lake, however, complete freezing of less saline surface layers has been instrumental in preventing survival of freshwater forms, a factor which cannot be important in Nitinat Lake.

In Hellefjord, one of the Norwegian fjords studied by Strøm (1936), the deoxygenated bottom waters may stagnate for several decades with little or no circulation and then be subjected to rapid, complete exchange during winter or early spring when the surface waters are cool, contain little fresh water, and are exposed to strong offshore winds. Such exchange brings the strongly deoxygenated bottom water which has a high H_2S content up to the surface and produces a catastrophic destruction of the fauna in upper layers of the fjord. Sudden circulation of the large volume of deoxygenated water, high in H_2S in Nitinat Lake, could result in widespread mortality of its fauna. However, this has probably been prevented by the length and other morphometric features of its sill.

ACKNOWLEDGMENTS

The assistance of T. G. Halsey on the first survey of Nitinat Lake is appreciated. Accommodation for both surveys was provided by McMillan, Bloedel and Powell River Limited at the Franklin River Camp where Mr Jack Bell was most helpful. The Moore-Whittington Lumber Company Limited kindly made available data on surface salinities of Nitinat Lake (Fig. 3). Dr G. L. Pickard arranged for salinity analysis at the Institute of Oceanography and provided valuable criticisms of the manuscript. Identification of specimens from Nitinat Lake by Mr C. Berkeley, Dr E. L. Bousfield, Mr T. H. Butler, Dr I. McT. Cowan, Mr D. M. Damkaer, Mr R. Drake, Miss G. A. Heron, Mr L. A. Hobson, Dr R. F. Scagel and Dr J. R. Stein is greatly appreciated.

REFERENCES

CLAPP, C. H. 1912. Southern Vancouver Island. *Canada, Dept. Mines Tech. Surv., Geol. Surv. Canada, Mem.*, No. 13, 208 pp.

ENGEL, R. A. 1962. *Eurytemora affinis*, a calanoid copepod new to Lake Erie. *Ohio J. Sci.*, **62**(5): 252.

GILMARTIN, M. 1962. Annual cyclic changes in the physical oceanography of a British Columbia fjord. *J. Fish. Res. Bd. Canada*, **19**(5): 921–974.

GURNEY, R. 1931. British fresh-water Copepoda. Vol. 1, Ray Society. Adlard and Son, London, 238 pp.

HERLINVEAUX, R. H. 1962. Oceanography of Saanich Inlet in Vancouver Island, British Columbia. *J. Fish. Res. Bd. Canada*, **19**(1): 1–37.

JOHNSON, M. W. 1961. The zooplankton of some Arctic coastal lagoons of northwestern Alaska with description of a new species of *Eurytemora*. *Pacific Sci.*, **15**(3): 311–323.

MCLAREN, I. A. MS, 1961. The hydrography and zooplankton of Ogac Lake, a landlocked fiord on Baffin Island. Ph.D. Thesis, Yale University.

MOHR, J. L., D. J. REISH, J. L. BARNARD, R. W. LEWIS AND S. R. GEIGER. 1961. The marine nature of Nuwuk Lake and small ponds of the peninsula of Point Barrow, Alaska. *Arctic*, **14**(4): 211–223.

MURRAY, J., AND L. PULLAR. 1910. Bathymetrical survey of the Scottish fresh-water lochs. Vol. 2, Part 2, Challenger Office, Edinburgh, 281 pp.

NORTHCOTE, T. G., AND W. E. JOHNSON. 1964. Occurrence and distribution of sea water in Sakinaw Lake, British Columbia. *J. Fish. Res. Bd. Canada*, **21**(5): 1321–1324.

PICKARD, G. L. 1961. Oceanographic features of inlets in the British Columbia mainland coast. *J. Fish. Res. Bd. Canada*, **18**(6): 907–999.

1963. Oceanographic characteristics of inlets of Vancouver Island, British Columbia. *J. Fish. Res. Bd. Canada*, **20**(5): 1109–1144.

STRØM, K. M. 1936. Land-locked waters. Hydrography and bottom deposits in badly-ventilated Norwegian fjords with remarks upon sedimentation under anaerobic conditions. *Skrifter Norske Videnskaps-Akad. Oslo*, **1**(7): 1–85.

TROLLE, A. 1913. Danmark-Ekspeditionen til Grønlands Nordøstkyst 1906–1908 under ledelse af L. Mylius-Erichsen. Bind I, II. Hydrographical observations from the Danmark Expedition. *Medd. om Grønland*, **41**: 271–426.

WILLIAMS, P. M., W. H. MATHEWS AND G. L. PICKARD. 1961. A lake in British Columbia containing old sea-water. *Nature*, **191**: 830–832.

Club Cells and Granular Cells in the Skin of Lamprey[1]

By Wolfgang Pfeiffer[2] and T. F. Pletcher[3]

Institute of Fisheries
University of British Columbia, Vancouver, B.C.

ABSTRACT

The club and granular cells in the skin of the lamprey appear to be two forms of the same cell, with the club cells developing into granular cells. Granular cells discharge their content on the surface of the skin. Granular and club cells do not contain mucus. Lampreys and their larvae are rarely found in stomachs of salmonids or other fish, and feeding experiments show that many fish will not eat lampreys and ammocoetes. A distasteful secretion from the granular cells of the skin is suspected of being biologically significant in protecting the lamprey from predacious fish.

INTRODUCTION

Stomach analyses of various fish from the Salmon River near Langley, British Columbia, revealed that lampreys, although abundant, were rarely eaten by other species of fish. Lampreys appear to have some protection from predacious fish, and because of the unique structure of their skin, this was suspected of secreting a noxious substance.

In several different respects, the skin of the lamprey is unique among vertebrates. It is scaleless, possesses club cells and granular cells that are very different from those of true fishes (Gnathostomata), has a ciliated epidermis, and takes water up at a faster rate than that of any other aquatic vertebrate (Hardisty, 1954). Specialized granular cells (*Kornerzellen*), club cells (*Kolbenzellen*), and mucous cells (*Schleimzellen*) were described by the histologists of the mid-nineteenth century but their relationships and functions were not clearly understood (Schnakenbeck, 1955; Grassé, 1958). The present study was designed to test the hypothesis that the unique granular and club cells produce substances of a protective nature.

The function of the club cells and granular cells in lampreys is unknown. In the older literature it is suggested that the club cells of the lamprey are fat cells, mucous cells, or even sensory cells. The granular cells were first described as secretory and sensory cells. However, both cell types lack innervation and therefore are not sensory cells although they may secrete substances to the exterior. Pfeiffer (1960), in describing the club cells and the granular cells of the European lamprey *Petromyzon fluviatilis* L., assumed that they represent different developmental stages of the same cell type, i.e. that club cells are young granular cells.

[1]Received for publication January 27, 1964.
[2]Present address: Zoologish-vergl. anatomisches Institut der Universität Zürich, Zürich (Switzerland).
[3]Present address: Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

FIGURES 1–5

Sections taken through the skin of lampreys from the first two myotomes posterior to the last gill opening. Fixed with Bouin's fluid, sectioned at 5/μ and stained with Azan's technique. **c**, club cell; **e**, epidermal cell with mucus; **g**, granular cell; **p**, pore of granular cell; **t**, transitional form of club cell.

FIG. 1. *Lampetra planeri* ammocoete, 110 mm, × 1100.

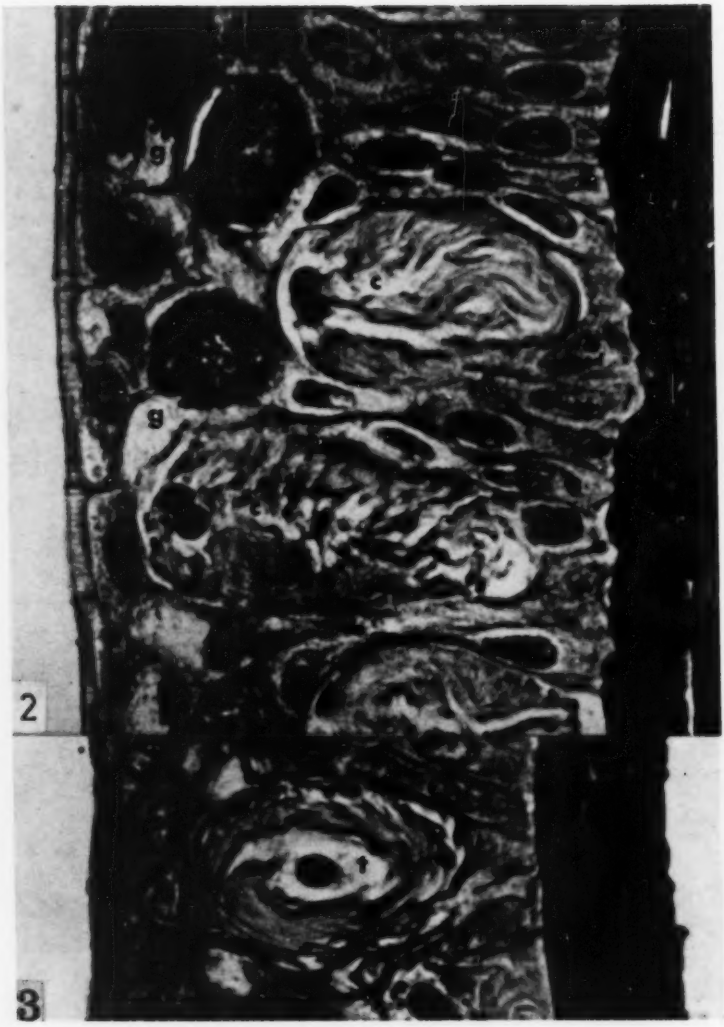


FIG. 2. *Lampetra planeri* ammocoete, 100 mm, × 1100.

FIG. 3. *Lampetra planeri* ammocoete, 90 mm, × 1100.

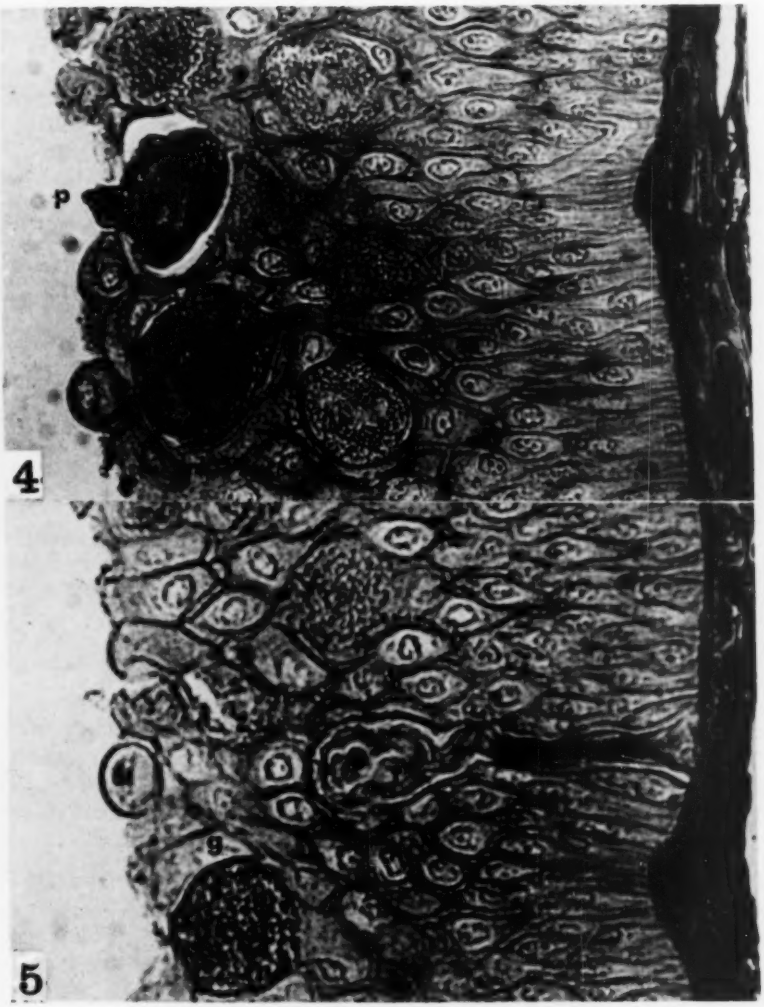


FIG. 4. *Entosphenus tridentatus* adults, × 563.

FIG. 5. *Entosphenus tridentatus* adults, × 563.

RESULTS

Histological Observations

Sections of skin of the British Columbian ammocoetes *Lampetra planeri* (Bloch) from the Salmon River (Fig. 1 and 2) and adult *Entosphenus tridentatus* (Gairdner) from the Stamp River (Fig. 4 and 5) were fixed with Bouin's fluid and stained with Azan's technique (Humason, 1962). Figure 1 shows the position of the club cells (c) at the base of the epidermis and the granular cells (g) at the surface of the ammocoete skin. Cells that are apparently transforming from club cells to granular cells can be seen in Fig. 3 and 5 (t) and occupy a position in the center of the epidermal layer. Small ammocoetes possessed fewer granular cells in their skin than did large ammocoetes. Pores (p) leading from the granular cells to the exterior can be seen in Fig. 1 and 4. Figure 3 shows what appear to be inter-cellular connections between the club cell and the surface. Epidermal cells (e) covered with a striated cuticle form the surface layer of the skin of ammocoetes. Adult lamprey shed the epidermal layers as is shown in Fig. 4 and 5.

Sections of lamprey skin were preserved in Bouin's fluid and stained with P.A.S. (periodic acid – Schiff) and toluidine blue (Pearse, 1962). Mucus was present in the upper two layers of the epidermal cells (Fig. 1, e), but the granular cells and club cells did not contain mucus.

Sections of ammocoete skin stained with P.A.S., celestine blue, Mayer's haemalum, and alcohol blue (Pearse, 1962) showed that the granular cells and club cells contained a substance that stained in a similar manner to protein fibers.

Experimental Observations

Stomach analysis of 20 coho salmon fry (*Oncorhynchus kisutch*), 5 rainbow trout fry (*Salmo gairdneri*), 5 cutthroat trout (*Salmo clarki clarki*), and 10 redside shiners (*Richardsonius balteatus*) from the Salmon River revealed no incidence of lamprey remains. Hartman (personal communication) examined "hundreds" of salmonid stomachs from the Salmon River and found no lamprey remains.

The authors tasted live ammocoetes on numerous occasions and found that the skin is not distasteful when the ammocoete covered with mucus is placed on the tongue. However, when the ammocoete is pressed between the teeth and then placed on the tongue a bitter unpleasant taste is evident. Presumably, the distasteful or noxious substance in the skin does not come from the mucus, but is forced from the granular cells or club cells when the skin is compressed or bitten.

Feeding experiments were conducted to see if fish would eat lamprey. Lamprey eggs (which ordinarily would have been buried in the gravel) were eaten when presented to salmonid fry in both natural stream conditions in the Salmon River and in an experimental tank. Newly hatched ammocoetes were eaten on about half of the occasions when they were fed to fry. Emergent

ammocoetes commonly leave the gravel at night, float with the current, and are deposited and bury in the soft bottom muds where current is reduced (Pletcher, MS, 1963). Thus emergent ammocoetes may escape detection by the fry since they may not be seen or smelled.

Ammocoetes (30–130 mm) were introduced, before regular feeding hours, to the surface of a hatchery trough containing 900 artificially reared coho. Annelid worms approximately the same size as the ammocoetes were introduced into the tank before and after feeding with ammocoetes. An ammocoete was taken into the mouth of the first fry making contact with it but was immediately rejected. In most instances an ammocoete that was rejected was immediately tasted by another fry and again released. Each ammocoete was tasted by at least 50 fry during the 30-min feeding periods. A skinned ammocoete was introduced in a similar manner as the previous specimen, but it was always eaten by the fry making contact with it. The skin from the skinned ammocoete was introduced but it was never eaten although it went through the same tasting and release procedure as the whole ammocoete. The worm that was introduced at the conclusion of each test was always eaten. No intact ammocoetes or ammocoete skins were eaten during the five tests performed at daily intervals.

A second experiment was performed in which the same lamprey–worm combinations were fed to five Salmon River coho fry and two cutthroat trout. The results were similar but the number of attacks was reduced at each feeding (possibly due to the learning by the fry). Ten redside shiners, ten threespine stickleback (*Gasterosteus aculeatus*) and five prickly sculpins (*Cottus asper*) from the Salmon River were also fed ammocoetes, but all showed the same reaction to whole ammocoetes as exhibited by the fry. Adult rainbow trout (*Salmo gairdneri*) exhibited the same negative response as the salmonid fry, when 5-cm pieces of adult *Lampetra planeri* were fed to them in a large outdoor tank. However, the squawfish (*Ptychocheilus oregonense*) and the blind cavefish (*Anoptichthys jordani*) ate ammocoetes readily and showed no aversion.

DISCUSSION

In the skin of *Lampetra planeri* the club cells lie near the surface of the skin. Various intermediate or transitional stages of development are positioned between these two cell types, in the middle of the epidermis (Fig. 3 and 5, t). The migration of the nucleus from a position at the top of the club cell to a central location in the granular cells corresponds to the migration of the nucleus in the epidermal cells (Pfeiffer, 1960). The shape of club cells and granular cells varies from a club shape to a spherical shape. Both club and granular cells have pores to the surface of the skin and lack mucus. This helps to substantiate Pfeiffer's belief that club cells and granular cells in lampreys are different development stages of the same cell type.

Perlmutter (1951) kept ammocoetes and eels in an aquarium and recorded that the eels burrowed in the mud and ate the ammocoetes. Thomas (1962)

noted lamprey remains in brown trout in West Wales to be less than 0.1% of the food and then only during the month of May. However, he found that eels preyed on ammocoetes during June to September (1.1–2.2% of the food). Churchill (1947) found no evidence of lamprey remains in 200 sucker stomachs, and in 300 trout stomachs there were only five incidences of lamprey (spawned-out adults) in the stomach. These lampreys may have been eaten because the epidermis was sloughed off after spawning (Applegate, 1950). Lamprey remains were reported in two white sturgeon (*Acipenser transmontanus*) in the lower Fraser River (Semakula, MS, 1963). Certain fish as the eel, sturgeon, and squawfish do not react to the protective substance in the lamprey's skin. However, salmonids do not eat lamprey in many stream environments. The feeding habits of the predator, the burrowing habits of the lampreys, or the protective nature of the lamprey's skin could account for the lack of lampreys in the stomachs of fish in the stream environment.

The presence of noxious substances in the skin of lampreys would greatly reduce the mortality due to predation by fish. Many fish "taste" and hold their prey in their mouth before swallowing. The noxious substance secreted by lamprey skin when bitten by fish apparently provides the lamprey with a protective mechanism. This may be a factor in their explosive increase in the Great Lakes (McLain, 1951).

ACKNOWLEDGMENTS

The study was performed while the senior author had a postdoctoral fellowship from the National Research Council of Canada. Drs W. S. Hoar, P. A. Larkin, and J. D. McPhail kindly read the manuscript. Dr C. V. Finnegan gave valuable suggestions and assistance with the histological preparations. We acknowledge thankfully all help received.

REFERENCES

Applegate, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus* in Michigan. *U.S. Fish Wildlife Serv., Spec. Sci. Rept., Fisheries*, No. 55, 237 pp.

Churchill, W. S. 1957. The brook lamprey in the Brule River. *Trans. Wisconsin Acad. Sci.*, **37**: 337–346.

Grassé, P. 1958. Poissons. Traité de Zoologie, Vol. 13(1). Masson, Paris.

Hardisty, M. W. 1954. Permeability to water of lamprey integument. *Nature*, **174**: 1360.

Humason, G. L. 1962. Animal tissue techniques. W. H. Freeman & Co., San Francisco and London.

McLain, A. L. 1951. Diseases and parasites of the sea lamprey *Petromyzon marinus*, in the Lake Huron basin. *Trans. Amer. Fish. Soc.*, **81**: 94–100.

Pearse, A. G. 1962. Histochemistry, theoretical and applied. Little, Brown and Company, Boston, Mass.

PERLMUTTER, A. 1951. An aquarium experiment on the American eel as a predator on larval lampreys. *Copeia*, 1951(2): 173–174.

PFEIFFER, W. 1960. Über die Schreckreaktion bei Fischen und die Herkunft des Schreckstoffes. *Z. Vergl. Physiol.*, **43**: 578–614.

PLETCHER, T. F. MS, 1963. The life history and distribution of lampreys in the Salmon and certain other rivers in B.C., Canada. Master's Thesis, Dept. of Zoology, University of British Columbia.

SCHNAKENBECK, W. 1955. Pisces. *In* Kükenthal's "Handbuch der Zoologie", Part 1: 6, pp. 571–582.

SEMAKULA, S. MS, 1963. The age and growth of the white sturgeon (*Acipenser transmontanus*) of the Fraser River, B.C., Canada. Master's thesis, Dept. of Zoology, University of British Columbia.

THOMAS, J. D. 1962. The food and growth of brown trout (*Salmo trutta* L.) and its feeding relationship with the salmon parr (*Salmo salar* L.) and the eel (*Anguilla anguilla* L.) in the River Teify, West Wales. *J. Animal Ecol.*, **31**: 175–205.

Reflectivity of the Chorioidal Tapeta of Selachians[1]

By J. A. C. Nicol

Marine Biological Laboratory
Plymouth, England

ABSTRACT

The reflecting layer or chorioidal tapetum in the eye of many selachians was examined to determine, especially, whether it is a set feature or whether it can be occluded.

Many selachians have a tapetum under the entire fundus of the eye. It consists of highly reflecting cells, towards the outer ends of which there is a layer of melanophores. In active pelagic sharks of the neritic zone (e.g. *Squalus*, *Mustelus*), the melanophores send out pigment over the reflecting cells so as to conceal them when the fish is illuminated; the pigment retreats in darkness. In benthic species of the neritic zone, notably *Scyliorhinus*, the fundus has a black ventral area; a tapetum occurs elsewhere and is not occlusible. The eyes of rays have a black ventral field, and pigment migration over the tapetum is slight. The tapetum is not occlusible in deep-sea squaloids and a chimaerid *Hydrolagus affinis*.

Reflectivity of the dark-adapted tapetum of *Squalus acanthias* amounts to about 85%. Full expansion of pigment in the light and retreat in darkness occupy about 2 hr in this fish.

Pieces of tapeta, freed of retinae, were mounted in Ringer solution, observed, and photographed by oblique illumination from above. The tapetal pigment migrates inwards over the reflecting plates in such preparations of tapeta from fishes that have occlusible tapeta.

The suggestion is offered that the tapetum is concealed, either by closure of the pupil or by migration of pigment, so as to avoid displaying eye-shine. Deep-sea squaloids, living in dimly lit environments, do neither.

INTRODUCTION

Most elasmobranchs have a tapetum lucidum or mirror in the innermost region of the chorioid of the eye immediately outside the choriocapillaris. The tapetum contains a single layer of plate-like cells which are highly reflecting and fixed in position. Their disposition relative to the retina is different in various parts of the eye. In the centre of the fundus they are parallel to the choriocapillaris and retina; away from the centre of the eye they become oblique to the retina, and the angle increases towards the ora where they approach the vertical. The histology of the tapetum lucidum and the arrangement of the reflecting plates have been described by Denton and Nicol (1964). In that paper it has been shown that the orientation of the reflecting plates is always such that they are approximately perpendicular to the light which reaches them.

At the base of the reflecting cells (i.e. lying immediately external to them) is a single layer of black pigmented cells; these bear pigmented processes which may extend over some part of the inner surfaces of the reflecting cells. Franz (1905, 1913), on the basis of some observations which he made on *Squalus acan-*

[1]Received for publication May 28, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

thias and *Galeorhinus galeus*, came to the conclusion that black processes of the underlying chorioidal pigmented cells, moving inwards, could conceal the shining tapetum. When eyes were placed in the light, the pigment moved inwards, covered the reflecting plates, and occluded the tapetum; in darkness the pigment retracted. Essentially these cells were behaving as polarized melanophores, having processes which extended centripetally, in one direction, inwards towards the centre of the eye (evidence reviewed by Nicol, 1963).

To Franz belongs the credit for discovering the process of occlusion which takes place in the selachian tapetum when the eye is illuminated, but apparently he made no systematic study nor experimental investigation of the process. Franz's observations on the spur dog (*Squalus acanthias*) have been confirmed by Denton and Nicol (1964). The eye of a spur dog that has been in darkness for some time shines brightly; when the eye has been illuminated the inside of the eye becomes dark green or almost black. These changes are brought about by movement of pigment in processes of the chorioidal tapetal pigment cells, to and fro over the reflecting plates. Franz spoke of movement of pigmented processes, but Denton and Nicol favoured the idea of a movement of pigment in fixed processes. An occlusible tapetum has also been reported by Gilbert (1961) in the sharp-toothed shark *Negaprion* (species not stated, perhaps *queenslandicus*).

Despite the general and prevalent impression that an occlusible tapetum is ubiquitous among selachians, it has been demonstrated that the tapetum of the rough dog (*Scyliorhinus canicula*) does not alter in light and darkness (Nicol, 1961). In the spur dog, mentioned above, a tapetum lies under the retina everywhere. But in the rough dog the tapetum lucidum is restricted to part of the eye. The eye contains a large black ventral field, triangular in shape, with the apex extending slightly above the optic nerve, a bright fundus above and lateral to this region, and a narrow black band across the top of the eye, next to the ora. In much of the black ventral field there are no reflecting cells, and in the ventral field and in the black dorsal band black pigmented cells extend to the choriocapillaris. It is apparent, therefore, that at least two types of tapeta can be distinguished in selachians, according to whether they are occlusible or not.

Over the course of the past few years the eyes of various species of selachians and chimaerids have been examined as opportunity permitted, and their tapeta have been studied. In the English Channel, where many of the specimens used in this study were obtained, the rough dog is the common dogfish and, as we have already noted, its tapetum is not occlusible. Spur dogs occur from time to time, when pursuing pilchards, but many of the observations on spur dogs were made at the Marine Station, Millport, Scotland. In the Clyde Estuary the spur dog is the common dogfish, and is available in quantity. Specimens of deep-sea squaloids were examined on board R. V. *Sarsia* in the Bay of Biscay. In the following account the tapeta of various species of selachians are described. The process of occlusion has been followed in several species, but especially in spur dogs, and the results of this study are presented.

MATERIALS AND METHODS

The tapeta of the following species of selachians were examined: nursehound (*Scyliorhinus stellaris*), rough dog (*S. canicula*), blue shark (*Carcharhinus glaucus*), tope (*Galeorhinus galeus*), smooth hound (*Mustelus asterias*), spur dog (*Squalus acanthias*), other squaloids (*Deania calcea, Centrophorus squamosus, C. granulosus* and *C. coelolepis*), angel fish (*Squatina squatina*), electric ray (*Torpedo nobiliana*), thornback ray (*Raia clavata*), spotted ray (*R. montagui*), blonde ray (*R. brachyura*), small-eyed ray (*R. microocellata*), cuckoo ray (*R. naevus*), bordered ray (*R. marginata*), common skate (*R. batis*), and sting ray (*Dasyatis pastinaca*); also one species of deep-water chimaerid (*Hydrolagus affinis*).

For histological study, eyes were usually fixed in Bouin's fluid and sectioned in celloidin. Sections were stained with Ehrlich's haemotoxylin and eosin or lissamine violet AVS (British Drug Houses).

To examine fresh tapeta the following procedure was adopted. The fish was decapitated and the eyes were excised and placed in Ringer solution (made up according to a formula recommended by Nicholls, 1933). When the fish had been illuminated, the dissection was carried out in white light; when the fish had been dark-adapted, the dissection was carried out in red light of low intensity. The front of the eyeball was removed, the lens pulled out, and the eye was cut into radial segments. The vitreous humour was gently pulled away from each piece and the pieces were restored to Ringer solution. Soaking the pieces in Ringer facilitated subsequent removal of the retina. The retina was pulled off each piece, which was then ready for examination by incident light from above.

For observing and for photographing pieces of stripped tapeta a reflecting microscope was employed. The preparation was placed in a small chamber seated in the condenser mounting beneath the microscope stage. Focussing was carried out by raising or lowering the condenser mounting. Either the specimen was mounted dry (for immediate study) or it was covered with Ringer. The tapetum was illuminated from above by two midget fluorescent tubes of 4-w, 6 inches long, one on either side of the objective; the tubes were capped by reflectors of aluminium foil. On top of the microscope was placed a Reichert photomicrographic camera "Remica II", having a beam-splitting tube and a focussing telescope that allowed observation. In the microscope were a 10 × ocular and a Leitz 16-mm objective.

Measurement of the amount of light reflected by a piece of stripped tapetum was made by the apparatus described by Denton and Nicol (1962, 1964). The piece of tissue was mounted in a V-shaped chamber and covered with Ringer solution. It was illuminated unilaterally and diffusely by a lamp behind an opal (which scatters according to the cosine law). The holder containing the tissue and the adjacent opal could be moved horizontally beneath the objective of a microscope, which received light vertically from the opal or from the tissue, depending on which lay beneath it. The preparation was viewed vertically through a Leitz "Mikas" micro-attachment and the amount of light passing through the mi-

croscope was measured by a photomultiplier fixed over the top of the micro-attachment. All measurements of light reflected by the tapetum were made relative to the amount of light coming through an adjacent region of the opal. For these measurements a 6 × ocular and a Zeiss 18-mm objective were used.

Dogfishes of various species were dark-adapted by placing opaque patches over their eyes, or by holding them in aquaria in darkened rooms. Other fish were dark-adapted by keeping them in darkened rooms; some species, especially deep-sea squaloids, were captured at night and were examined immediately or held in darkened tanks. Because of the varied circumstances in which fish were examined, it was not always possible to standardize all environmental variables. Light-adapted eyes were obtained from fish which had been in daylight, or fish were illuminated by a 150-w tungsten bulb hung about 1 m above the tank. Tank temperatures were usually 15°C, and room temperatures were about 18°C.

OBSERVATIONS

Spur Dog, *Squalus acanthias*

The structure and the appearance of the tapetum of *Squalus acanthias* have been described elsewhere (Denton and Nicol, 1964). The tapeta of fish which had been in darkness for 2 hr or more were very bright (Fig. 1, F, G). The tapetum of a fish that had been illuminated for ½ hr showed streaks of black pigment extending some way across the reflecting plates of the tapetal surface (Fig. 1, H, J). After a fish had been illuminated for 2 hr, the pigment became extended so as to cover and obscure almost all the tapetum lucidum, and the surface appeared very dark (Fig. 1, A).

Course of pigment-migration. Dark-adapted and light-adapted spur dogs were placed in light or darkness, respectively, in order to follow the course of pigment-migration. Animals were sacrificed at intervals of 15 min, 30 min, 1, 1½, and 2 hr and some at longer intervals. After 20 min exposure to light, tapeta were moderately bright and chorioidal tapetal pigment was partially extended, covering about one-third of the reflecting surface (Fig. 1, H). After 1 hr in the light the tapetum was quite dark, the pigment was fairly well extended and covered a large part of the reflecting surface (three-quarters or more). Pigment processes had extended in length and increased in number (Fig. 1, J). Some eyes became no darker than this. More often the tapeta of fish which had been in daylight for 2 hr or more appeared very black and were almost completely occluded by fully expanded pigment (Fig. 1, A).

The tapeta of previously light-adapted spur dogs were still black after 50 min in darkness, but some retraction of pigment had occurred and a little reflecting background shone through. After 70 min in darkness appreciable withdrawal had occurred and about one-quarter of the reflecting surface was exposed. At 100 min the tapetum appeared bright and the pigment was largely withdrawn. Complete retraction of chorioidal tapetal pigment occurred in 2 hr or a little longer (Fig. 1, A to G).

From these observations it was concluded that chorioidal tapetal pigment in the light became greatly expanded so as to cover most of the tapetum in 1 hr, and fully expanded in 2 hr. In darkness chorioidal tapetal pigment became slightly retracted in 1 hr, greatly retracted in 1½ hr so as to expose most of the reflecting tapetum, and fully retracted after 2 hr. The complete change from bright tapetum to black tapetum on transferring an animal from darkness to light, and from dark tapetum to bright tapetum on transferring from light to darkness occupied about 2 hr. These changes may be compared with those recorded by Gilbert (1961) for the shark *Negaprion*. In sunlight the tapetum lucidum of this shark became occluded in less than an hour, and in darkness it became exposed after 4 hr.

MEASUREMENTS OF REFLECTIVITY. The reflectivity of isolated pieces of tapeta was measured with an apparatus designed for that purpose (Denton and Nicol, 1962, 1964). All measurements were made on pieces from the central fundus above the optic nerve. Each piece was mounted so that its ventral edge (i.e. the edge that would be closest to the centre of the eye when it was *in situ*) abutted against the illuminated opal. Tank temperatures were 9.7 to 10.2°C.

In an eye that had been in darkness overnight, the tapetum was bright and the pigment was retracted. Reflexion was 84% and 86.7% (two determinations). When the tapetum was turned through 90° so that its lateral edge now abutted against the opal, the reflexion was 35.7% in that direction; when it was turned through 180° so that its dorsal edge lay against the opal, the reflexion in that direction was 16%.

These differences arise because of the slope of the reflecting plates, and the matter is discussed elsewhere (Denton and Nicol, 1964).

In an eye from a fish that had been in the light all day, the tapetum was very dark, and the pigment was fully extended. Reflexion was 1.8%.

Opaque patches were placed in the eyes of fishes that had been in daylight for several hours; the fish were killed at intervals and reflexion was measured. These experiments were done so as to obtain information about the change of reflectivity that takes place after the fish passes from light to darkness (Fig. 1, B to F). The results are shown in Table I.

TABLE I. Changes in appearance and reflectivity of chorioidal tapeta of *Squalus acanthias* when fish that had been in daylight for several hours were subjected to darkness for various periods of time.

Time in darkness	Appearance of tapetum	Reflexion (angle, 62°)
min		*in %*
20	Moderately dark, pigment well extended	18.8–20
50	Fairly bright, pigment moderately well extended	40.4
60	Fairly bright, pigment fairly well extended	34
70	Fairly bright, pigment partially extended	50
75	Bright blue, pigment slightly extended	62
95	Bright, pigment completely retracted	88

HISTOLOGICAL OBSERVATIONS. Some of the preparations, which were examined and photographed, were preserved for histological examination. In eyes which had been in darkness, the pigment was withdrawn into the cell body of the pigment cell; and in eyes which had been exposed to light, the pigment was extended in various degrees between and over the reflecting plates (Fig. 2). When the eyes had been in light for a long time, and the tapetum was very dark and showed the pigment well extended, then, in sections the pigment was extended distally over the plates and beneath the choriocapillaris.

PIGMENT MOVEMENT IN ISOLATED TAPETA. Observations were made on the behaviour of chorioidal tapetal pigment in pieces of isolated tapeta, taken from light- and dark-adapted fishes. In these preparations the retinae were removed and the isolated pieces of tapeta were kept in light or darkness. In one series of observations, for example, the eyes were removed from a spur dog that had been in darkness for several days. The retina was stripped off and a piece of tapetum was mounted in Ringer for continuous microscopic examination and was left in the light. The temperature was 18.5°C. This fish was killed at 10.00 a.m., and the tapetum was mounted and examined at 10.10 a.m. (10 min after death). It was bright and shiny and only an occasional pigmented process was visible. At 10.20 a.m. (20 min) about ten times as many pigmented processes were visible, but the pigment was still only slightly expanded. Further pigmented processes began to appear, the pigment continued to expand, and between 35 and 45 min the tapetum appeared fairly dark. By 60 min the pigment had extended so as to cover a large part of the tapetal surface and the tapetum appeared about as dark as it does in the eyes of fish exposed to daylight. Expansion of pigment continued thereafter and, by 180 min, the tapetum had become so dark that only occasional small flecks of light could be seen in the microscopic field. This is the condition found in tapeta of fish exposed to bright sunlight for several hours.

Microscopic sections were prepared of some of these stripped tapeta. The pigment was usually stripped off cleanly from the pigment epithelium (which was not unexpected since the best preparations were selected for investigation). In some places, or throughout some preparations, the pigment epithelium was missing as well (exposing the choriocapillaris). In other preparations the tips of the outer segments were left behind in some places. In sections of tapeta, from which the retinae had been removed 2 hr previous to fixation, the pigment was fully extended over the tapetal plates (Fig. 2, A).

SMOOTH HOUND, *Mustelus asterias*

Smooth hounds were light-adapted and dark-adapted in aquarium tanks (temperature 15°C). In eyes of specimens held under artificial illumination for 1½–3 hr the tapeta were dark and the chorioidal tapetal pigment was well extended, in large part or completely. The tapeta of other animals held in darkness for 2 hr or more were bright and shiny and the chorioidal tapetal pigment was retracted.

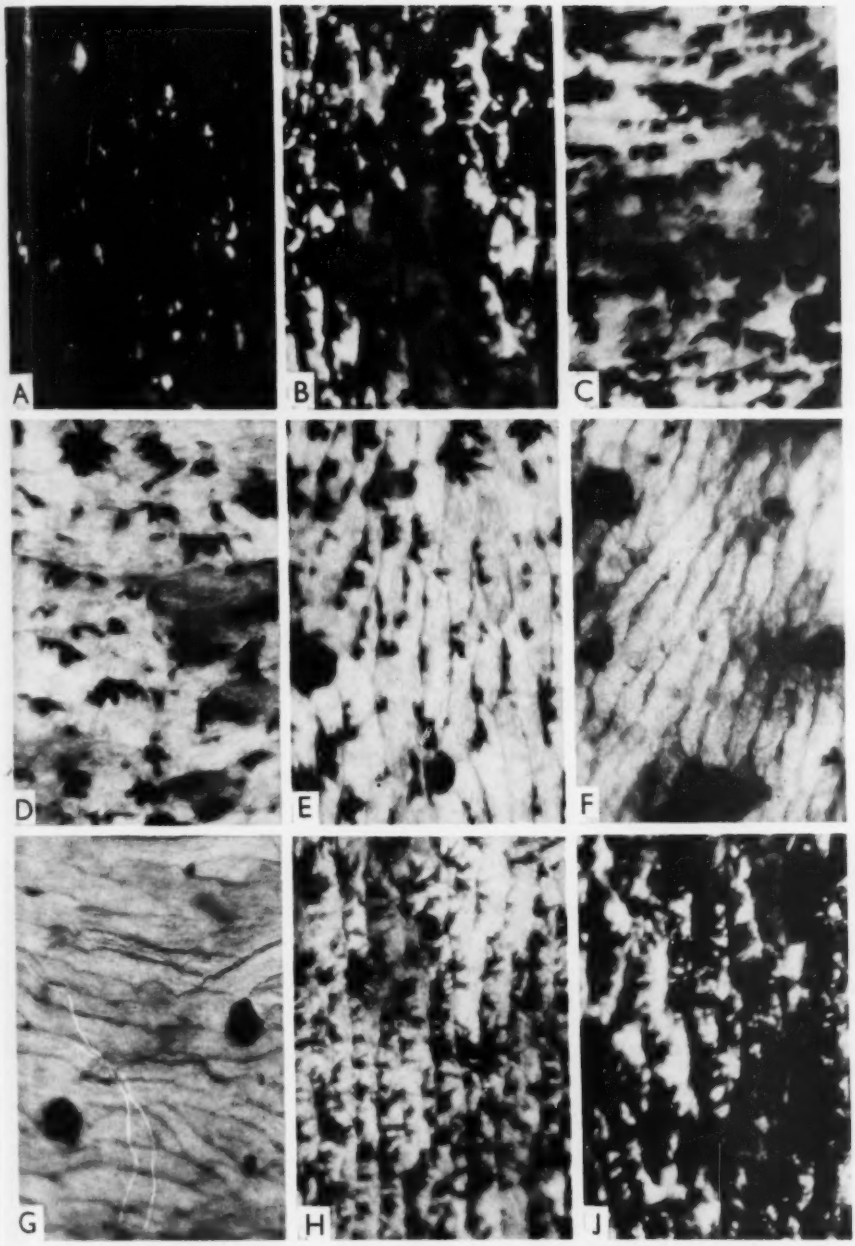


FIG. 1. Surface views of isolated tapeta of *Squalus acanthias*; photographed by reflected light × 160. **A.** Tapetum of normal fish, which had been in daylight all morning. **B.** Tapetum from an eye from which light had been excluded for 20 min. Reflectance 18.8%. **C.** Tapetum in darkness for 1 hr. Reflectance 34%. **D.** Tapetum in darkness for 1 hr, 15 min. Reflectance 62%. **E.** Tapetum in darkness for 1½ hr. **F.** Tapetum in darkness for 2 hr. **G.** Tapetum of normal fish which had been in darkness all day. **H.** Tapetum of a normal fish which had been exposed to light for 20 min. **J.** Tapetum exposed to light for 1 hr.

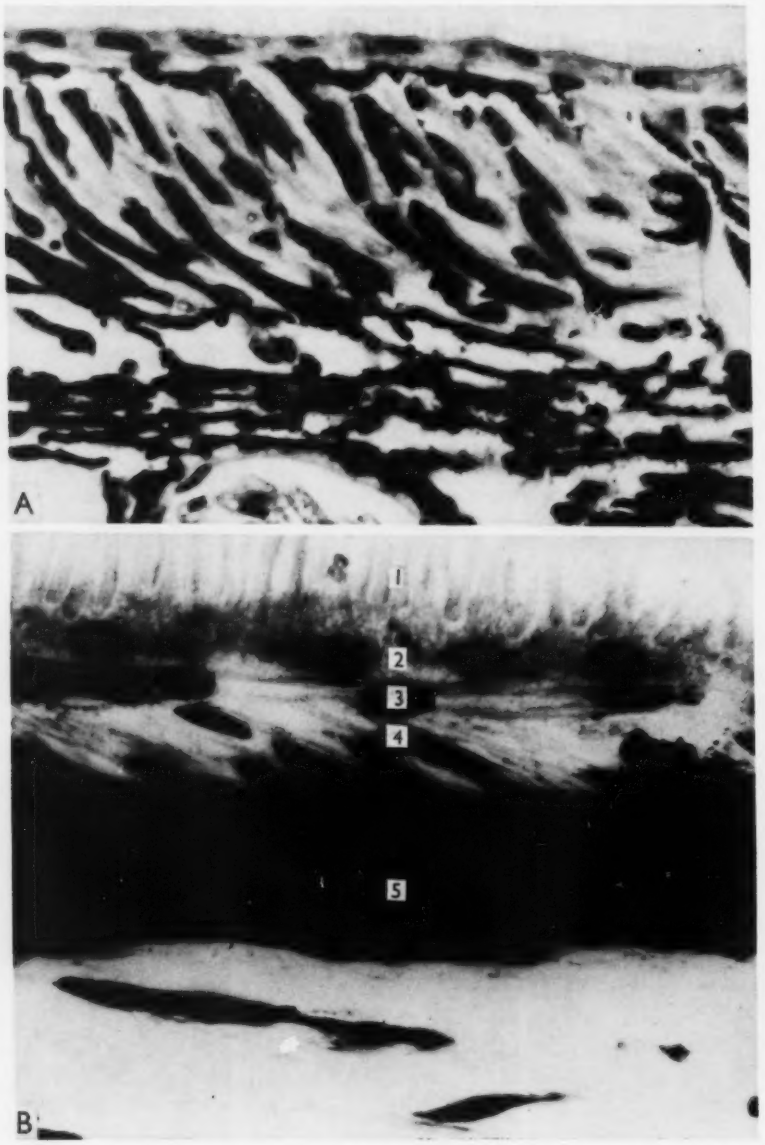


FIG. 2. Photographs of sections through the chorioidal tapeta of *Squalus acanthias*. A. Piece of stripped tapetum kept under observation for 2 hr. It was very dark and the pigment was well extended. × 600.

B. Eye from a dark-adapted fish. × 975. *Legend*: 1, rods; 2, pigment epithelium; 3, choriocapillaris; 4, tapetum lucidum; 5, chorioid layer outside the tapetum.

Nicol — J. Fish. Res. Bd. Canada

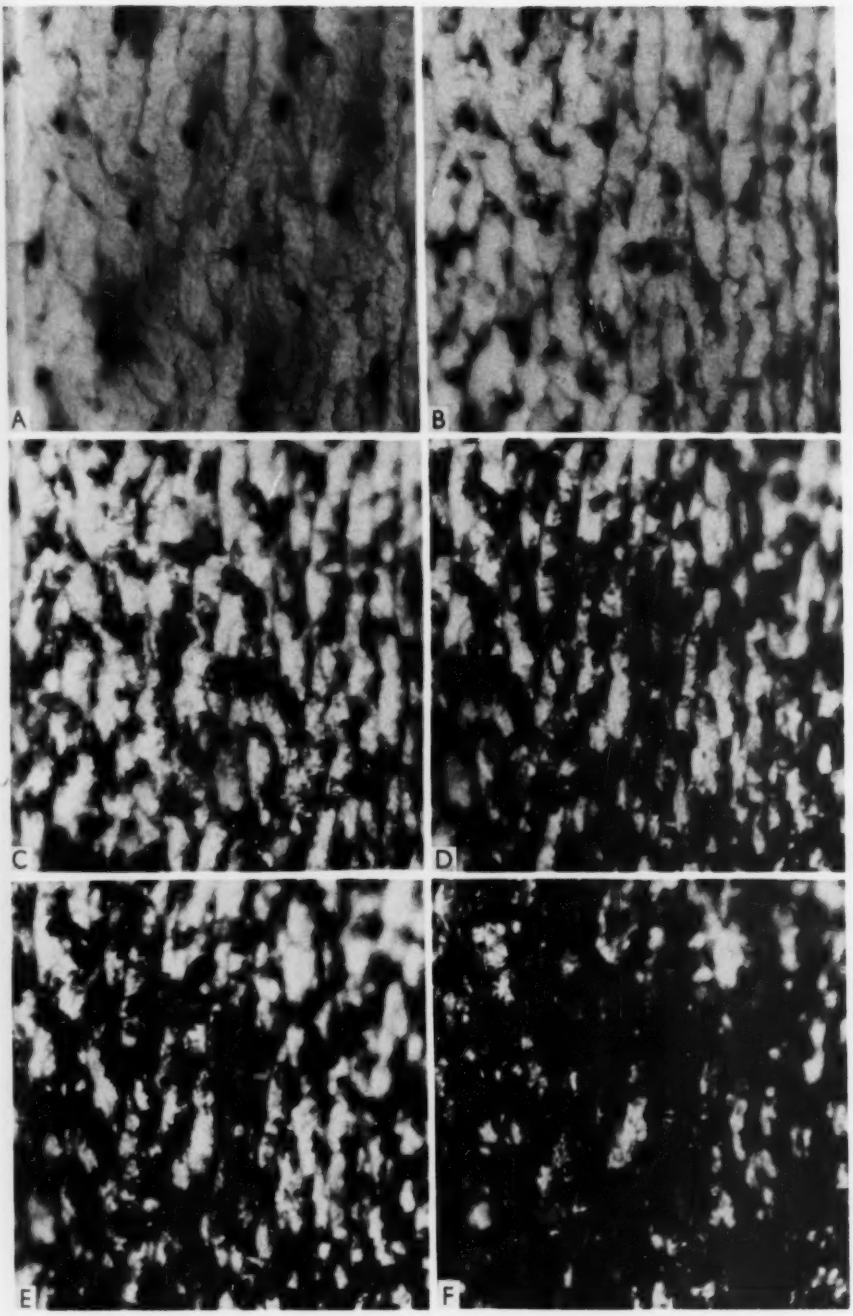


FIG. 3. A sequence of photomicrographs showing the course of pigment extension in a piece of stripped tapetum from a dark-adapted smooth hound *Mustelus asterias*. The preparation, in Ringer, was kept illuminated and photographed at intervals. Room temperature 18°C. Magnification, × 130.

A. Freshly mounted tapetum; large black spots are loci of blood vessels. **B.** 15 min. **C.** 30 min. **D.** 50 min. **E.** 1 hr. **F.** 2½ hr later.

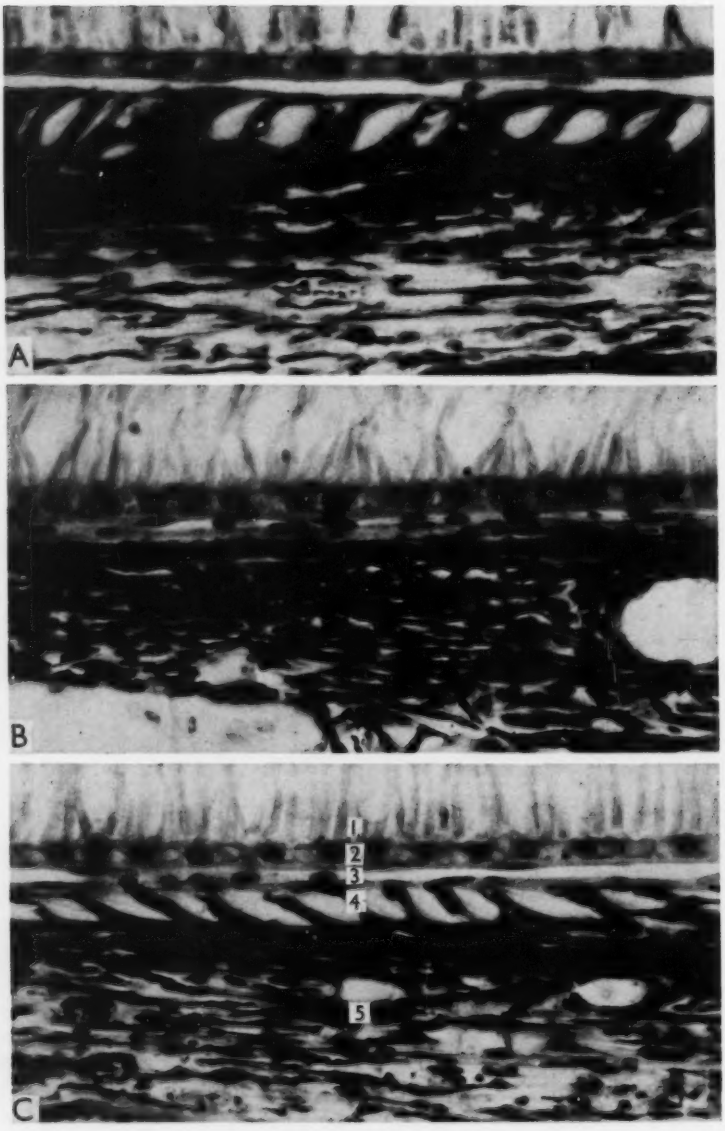


FIG. 4. Photographs of sections through the eye of an electric ray, *Torpedo nobiliana*. The fish had been in daylight and was light-adapted. Vertical transverse sections. × 385 **A.** dorsal; **B.** central; **C.** ventral fundus. *Legend:* 1, rods; 2, pigment epithelium; 3, choriocapillaris; 4, tapetum lucidum; 5, chorioid layer outside the tapetum.

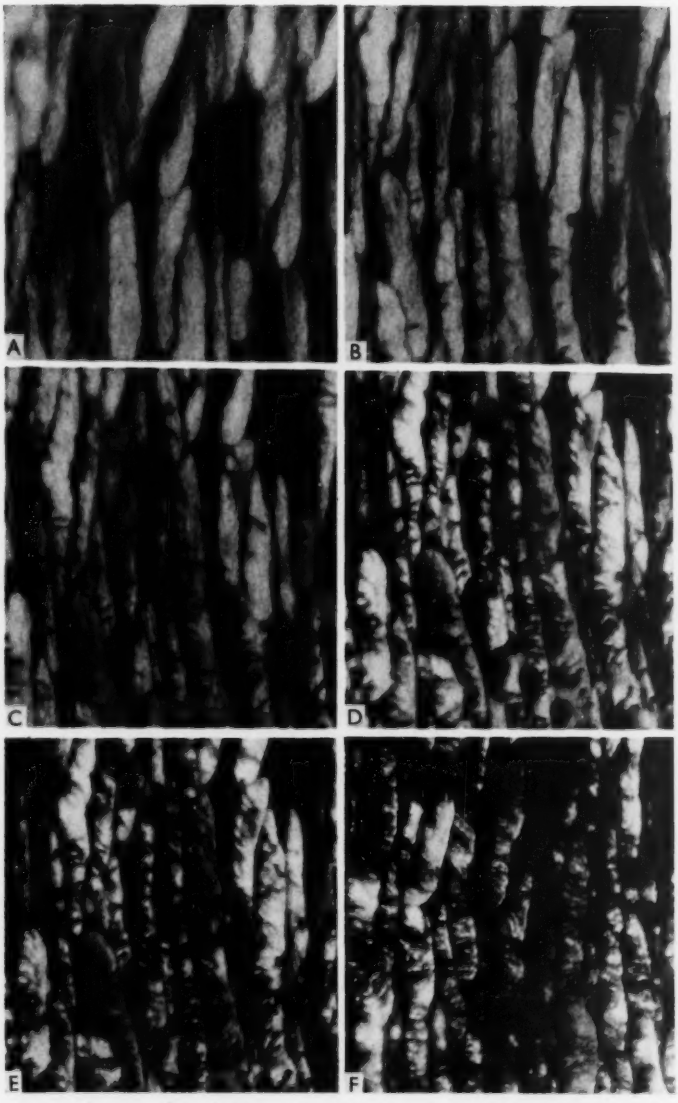


FIG. 5. Photographs of the surface of the tapetum of the ray *Raia clavata*. The preparation was obtained from the eye of a dark-adapted fish. The retina was stripped from a piece of the eye, and the stripped tapetum was mounted in Ringer on the reflecting microscope, and illuminated laterally from above. Initially no pigment was visible and a slow emergence and spread of chorioidal tapetal pigment took place. The photographs, taken at selected intervals, show stages in the spread of pigment. Room temperature 18°C. **A.** Start, pigment withdrawn. **B.** 17 min later, slight spread. **C.** 39 min. **D.** 45 min. **E.** 1 hr, 55 min. **F.** 2 hr, 45 min. × 110.

Surface views of bright tapeta were marked faintly with elongate outlines, delimiting areas which correspond to the exposed inner faces of the reflecting plates. Scattered over the bright field were coarse black spots corresponding to black pigment cells in the walls of blood vessels breaking through to the overlying choriocapillaris.

Pieces of stripped tapeta from dark-adapted eyes were kept in Ringer in light and in darkness for 2–3 hr. The preparations initially had silvery tapeta on which no chorioidal tapetal pigment was visible. Strands of chorioidal tapetal pigment began to peep out after 15 min, advanced part way across the plates in ½ hr, and continued to expand so as largely to cover the plates in 1–2 hr (Fig. 3). The process of occlusion progressed to the same extent and at the same rate in stripped tapeta held in light and in darkness. The pigment moved out unidirectionally across the reflecting plates, in a direction leading towards the centre of the eye. The pigmented processes appeared greyer than those of *Squalus acanthias*.

Sections showed a tapetal organization closely resembling that found in the eye of *Squalus*. Immediately adjacent to the ora there was no tapetum lucidum, and a carpet of dense black chorioidal pigment lay outside the pigment epithelium (which is not pigmented). Adjacent and centrally to this region the tapetum lucidum began. At first the reflecting cells were vertical or nearly vertical; proceeding towards the centre of the eye they became less steep, and over a large area of the central fundus they lay parallel to the retina. Where the reflecting cells were oblique they sloped towards the centre of the eye. In dark-adapted eyes the pigment was fairly well extended about the periphery of the eye; in the central fundus it was withdrawn into the cell bodies. In light-adapted eyes the pigment extended distally towards the retina and spread centrally beneath the choriocapillaris; it tended to accumulate in the distal (inner) portions of the cell processes, beneath the choriocapillaris.

Blue Shark, *Carcharhinus glaucus*

Several large blue sharks were caught during the hours of daylight. The eyes of these light-adapted specimens were dark dusky green, and the tapeta were uniformly dark, almost black.

The tapetum had an organization closely resembling that described in *Squalus acanthias*. Reflecting plates were parallel to the retina in the central fundus, and sloped increasingly away from the centre of the eye. The slope of the plates was towards the centre of the eye. In sharks caught in sunlight, the pigment was fully expanded over the entire surface of the plates and it extended, furthermore, beneath the choriocapillaris. Unfortunately, no specimens were caught at night, but one specimen was secured at dusk, attended by overcast sky and drizzle. The chorioidal tapetal pigment in this animal was partially retracted into the cell bodies of the melanophores.

Although no fully dark-adapted blue shark was captured, there is little doubt that it possesses a complete tapetum lucidum that is capable of becoming entirely occluded by day, and exposed by night.

TOPE, *Galeorhinus galeus*

In eyes of dark-adapted tope the tapeta were bright and shiny. In tope kept in the light for 4 hr, the tapeta were dark and dusky green, deeper in the ventral fundus, perhaps because of overhead illumination. Microscopic examination of light-adapted, stripped tapeta showed that the pigment was well extended, practically covering the reflecting plates.

Pieces of stripped tapeta from dark-adapted fish were covered with Ringer and kept in light and in darkness. Under such conditions the pigment became well extended in 70 min (18°C).

Reflecting cells, seen in histologic sections, were parallel to the retinal surface in the central fundus. Away from the centre they lay obliquely to the surface, and became increasingly so towards the ora. Chorioidal tapetal pigment was retracted in dark-adapted eyes, and extended in light-adapted eyes. As the pigment migrated inwards it did so in a direction pointing towards the centre of the fundus.

ELECTRIC RAY, *Torpedo nobiliana*

Specimens of torpedo were killed after being in daylight for several hours, or in darkness overnight or longer. Whether illuminated or kept in darkness, the tapeta were bright and shiny. In one light-adapted eye, pigmented processes were seen to be just peeping out over the edges of the reflecting plates. Typical melanophores lay near the outer ends of the reflecting cells, and pigmented processes extended towards the choriocapillaris, without extending over the more exposed surface of the reflecting plates (Fig. 4).

STING RAYS, *Urolophus* and *Dasyatis*

Through the kindness of Dr Findlay E. Russell some eyes of sting rays, *Urolophus halleri*, were obtained from California. These animals had been kept in darkness for 1–4 hr before death. There was a single layer of reflecting cells outside the choriocapillaris under the whole fundus. These were arranged obliquely to the retina except for a small region in the centre of the fundus, where they were parallel to the surface of the retina. Melanophores were present: in the dorsal and central fundus pigment was retracted; ventrally, below the optic nerve, the tapetal pigment was extended. There has been no opportunity of examining fresh tapeta or light-adapted eyes.

One specimen of *Dasyatis pastinaca* was examined, which had been in daylight. The ventral fundus, up to and slightly above the optic nerve, was heavily speckled with black, thinning out dorsally. The fundus was dusky olive green, with much dark speckling. In sections the tapetal pigment seemed to be well expanded.

Sting rays are infrequent at Plymouth, and the information secured is too scanty to permit generalization about the nature of the tapetum. So far as it goes it suggests that the eye of the sting ray has a pigmented ventral field, and that some occlusion of the central and dorsal fundus takes place in daylight.

NURSEHOUND, *Scyliorhinus stellaris*

The tapetum of the nursehound closely resembled that of the rough dog *Scyliorhinus canicula*. It is absent from a black ventral field extending up to the optic peduncle. Above and on either side of this area, a bright shiny tapetum occurred. A black ventral band occurred at the top of the eye, adjacent to the iris. Melanophore-like cells occurred at the outer margin of the reflecting layer, but they were non-motile. No excursion of pigment occurred when the eye was exposed to light, neither did the pigment expand when the retina was stripped off a piece of tapetum.

ANGEL FISH, *Squatina squatina*

An angel fish kept in darkness overnight had an open pupil and a bright tapetum on which no tapetal pigment was visible. Other fish, in daylight, had the pupils closed; the tapeta were bright blue, and some black speckling occurred in the ventral field. When examined microscopically, pigmented processes were seen to be just protruding from the edges of the reflecting plates.

Sections showed that a layer of reflecting plates lay outside the choriocapillaris under the whole fundus. In the central fundus they lay parallel to the surface of the retina; away from the centre of the eye they became oblique, and near the periphery of the eye they were almost vertical to the retina. In sections of the eye of an angel fish that had been exposed to sunlight, the chorioidal tapetal pigment was well extended, reaching the choriocapillaris; in sections from a dark-adapted eye the pigment was retracted, especially in the central fundus.

Pieces of stripped tapeta from light-adapted and from dark-adapted fish were examined in Ringer, and were kept illuminated for several hours. In both kinds of preparations a small amount of pigment-expansion occurred, but not enough to darken the tapetum, nor to conceal more than a small fraction of the reflecting surface.

RAYS, *Raia* spp.

In all the rays examined the fundus exhibited a black ventral field, triangular in shape, with the apex of the triangle extending up to the optic nerve. There was a fairly wide horizontal black band at the top of the fundus. The intervening region of the fundus (central and lateral parts) was bright and shiny. Inspection by the unaided eye revealed no marked difference between the tapeta of dark-adapted and light-adapted animals.

Histological examination showed that black chorioidal pigment extended up to the choriocapillaris in the black ventral field. In the bright region of the fundus there was a row of melanophores at the outer ends of the reflecting cells. In the region of the black dorsal band the pigment of these melanophores was expanded and extended inwards over the surface of the reflecting cells to the choriocapillaris.

In the eyes of dark-adapted rays the chorioidal tapetal pigment was retracted in the central fundus and was not visible. But in the eyes of rays that had been in daylight the pigment was slightly extended in this region so as to conceal

a small fraction of the reflecting surface. A corresponding picture was presented in sections: the pigment was retracted into the cell body in sections of dark-adapted eyes; it extended over the reflecting plates and beneath the choriocapillaris in sections of light-adapted eyes.

Pieces of stripped tapeta from light-adapted and dark-adapted rays (*R. clavata*, *R. brachyura*, *R. montagui*) were immersed in Ringer and were kept, some in light, others in darkness. Extension of pigment usually took place in these preparations, irrespective of whether they were kept dark or illuminated (for periods up to 4½ hr). It was slight to moderately extensive, but never enough to cover the tapetum completely; often the pigment emerged sufficiently to pass about a third or half way across the exposed inner surfaces of the reflecting plates (Fig. 5).

The eyes of rays are provided with an opercular flap that quickly descends over the pupil when the eye is illuminated. One interesting specimen of a thornback ray was found in which the opercular flap was deficient in one eye so that that pupil could not be closed; in the other eye the pupil was covered normally. This ray was illuminated by daylight for 2 hr. The tapeta of both eyes appeared the same: they were moderately bright and the pigment was slightly extended.

It was concluded that a slight extension of chorioidal tapetal pigment took place in the light, an extension insufficient to conceal greatly the reflecting surface of the tapetum. Seemingly, this behaviour was an intrinsic characteristic of the eye, not a consequence of pupillary closure. That the chorioidal melanophores were capable of a considerable degree of migration was shown by the extensive excursion of pigment that sometimes took place in stripped tapeta.

DISCUSSION

On the basis of observations collected together in this paper, and those reported elsewhere, it is possible to recognize several kinds of chorioidal tapeta among chondrichthian fishes, namely elasmobranchs or selachians and holocephalans. This list, which is not intended to be finite, may serve as a basis for discussion.

Occlusible tapetum. This kind of tapetum is found in active pelagic sharks living in well-illuminated waters. It lies behind most of the retinal lining of the eye, and its bright surface becomes concealed by a migration of pigment over it, when the eye is illuminated.

Non-occlusible tapetum occupying the whole fundus. Deep-sea squaloids, *Deania*, *Centrophorus* and a chimaerid, *Hydrolagus affinis* have bright tapeta lucida which occur under the entire fundus. These tapeta are permanently bright and non-occlusible.

Non-occlusible tapetum occupying part of the fundus. This occurs in some benthic selachians of the neritic zone, notably *Scyliorhinus*. The ventral part of the eye contains a black triangular patch, the ventral field. Here a tapetum lucidum is wanting. Elsewhere in the fundus a bright non-occlusible tapetum lucidum is present.

Partially occlusible tapetum. This occurs in various benthic selachians of the neritic zone. It is characterized by a slight or partial extension of the chorioidal tapetal pigment in the light, but the excursion is insufficient to cover much of the tapetal surface. In some species, e.g. *Squatina*, the tapetum extends over the whole eye; in others, notably *Raia*, a black field replaces the tapetum in the ventral fundus.

As shown elsewhere (Denton and Nicol, 1964), the retinae of sharks which live in well-illuminated waters possess visual pigments (rhodopsins) that occur in fairly low optical density. In general, they absorb about half the incident light reaching them and, since about 85% of the light transmitted through the retina is reflected by a bright tapetum, another 22% of incident light is absorbed in its second passage through the retina. If the optical density of the rhodopsin was so high that most of the light reaching the retina was absorbed, a tapetum lucidum would have little practical significance. It does make sense, however, when operating conjointly with a retina in which the density of visual pigment is low. Deep-sea squaloids and chimaerids have visual pigments of about twice the optical density as those of dogfishes of the neritic zone. Presumably, in the environment which they inhabit, where the illumination is highly attenuated daylight or feeble luminescence, an increase in rhodopsin concentration is of considerable marginal significance.

What, then, is the advantage of concealing the tapetum lucidum? Benthic species of the neritic zone usually conceal the tapetum by closing the pupil, e.g. *Scyliorhinus*, *Raia*, *Torpedo*. This process is rapid, taking place in 5–15 min. The iris or the opercular flap, in the closed state, displays camouflage coloration. In these animals occlusion of the tapetum by migratory pigment is negligible or absent. Among pelagic sharks of surface waters, however, iris movement is usually slight or negligible, and the tapetum becomes concealed by inward excursion of migratory chorioidal tapetal pigment. It takes about 2 hr for the tapetum to be completely covered or exposed on transferring from darkness to light or vice versa. Such tapetal alterations probably can follow changing light intensities at dawn and sunset. By either means, one way or the other, the fish can obviate eye-shine. The latter is extremely conspicuous in a dark-adapted fish (with an open pupil and a shiny tapetum) when it is suddenly illuminated. Deep-sea squaloids and chimaerids also display conspicuous eye-shine when they are brought to the surface during daylight hours. These animals have large pupils that do not close when the eye is illuminated and have bright non-occlusible tapeta. The light is always weak in the regions where these fish dwell, and eye-shine in that environment is correspondingly slight.

The occlusible tapeta of selachians still present many interesting problems that await solution. Among them may be singled out the method of regulating or controlling the migration of the chorioidal tapetal pigment, and the influence of light intensity on the magnitude and rate of the response. The fact that the pigment always migrates inwards in stripped tapeta, whether they are kept in light or in darkness, has been mentioned. This behaviour certainly seems to point to the removal of some controlling agent. And in the course of these

observations it has been noticed that in those species in which tapetal occlusion occurs, the tapetum darkens to a much greater degree in bright than in weak light, but no systematic attempt has been made to explore this relationship.

REFERENCES

DENTON, E. J., AND J. A. C. NICOL. 1962. Why fishes have silvery sides; and a method of measuring reflectivity. *J. Physiol.*, **165**: 13–15.

1964. The chorioidal tapeta of some elasmobranch fishes (Chondrichthyes). *J. Marine Biol. Assoc. U. K.*, **44**: 219–258.

FRANZ, V. 1905. Zur Anatomie, Histologie und functionellen Gestaltung des Selachierauges. *Zena. Z. Naturw.*, **40**: 697–840.

1913. Sehorgan (Chorioidea, Selachier), pp. 166–169. *In* A. Oppel, [ed.] Lehrbuch vergl. mikr. Anat. Wirbeltiere, Part 7. Fischer, Jena.

GILBERT, P. W. 1961. The visual apparatus of sharks and its probable role in predation. 10th Pacific Science Congress (Honolulu), Abstracts of Symposium Papers, pp. 176–177, 1961.

NICHOLLS, J. V. V. 1933. The effect of temperature variations and of certain drugs upon the gastric motility of elasmobranch fishes. *Contr. Canadian Biol.*, **7**: 447–463.

NICOL, J. A. C. 1961. The tapetum in *Scyliorhinus canicula*. *J. Marine Biol. Assoc. U. K.*, **41**: 271–277.

1963. Some aspects of photoreception and vision in fishes. *Adv. Marine Biol.*, **1**: 171–208.

ADDENDUM

It has been possible to inspect the eyes of some fresh bathy benthic rays, *Raia richardsonii*, caught at 2000 m in the Bay of Biscay by Mr G. R. Forster. These fish were dead when brought to the surface in daylight. Their eyes much resembled those of the squaloids from deep water, described in this paper. Pupils were large, the operculum was vestigial and a bright tapetum occupied the whole fundus; there was no black ventral field. There is strong suggestive evidence that the eyes of these deep-water rays have the same features as those of the squaloids *Deania* and *Centrophorus*, features suitable for an environment of low light intensity.

Growth Rate of Central British Columbia Pink Salmon (*Oncorhynchus gorbuscha*)[1]

By R. J. LeBrasseur and R. R. Parker

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Pink salmon were sampled at various stages, as fry and fingerling in enclosed waters, as juveniles and subadults in the ocean and as maturing salmon in the commercial fishery. On the basis of length frequency data and from recapture measurements of marked and tagged individuals the instantaneous growth rate in length (g_l) for successive 30-day periods was computed. As a result three major growth stanzas were recognized. Following the entrance of fry into the estuary, growth was approximately exponential ($g_l = 0.559$) during an initial 40-day period. Fish increased in length from 3.5 to 8.4 cm. Thereafter, the instantaneous rate of growth gradually declined to a minimum in March ($g_l = 0.076$). During this time the length increased from 8.4 to 32.5 cm. The final growth period was marked by a rapid rate of increase in length in late April and early May ($g_l = 0.171$), followed by a declining rate of increase in length which was finally terminated after the fish had re-entered the coastal waters and the commercial fishery ($g_l = 0.041$). The length data were transformed to weight data from a generalized length–weight regression. During the initial 30-day period the instantaneous growth rate in weight, $g_w = 6.53$. From a value of $g_w = 2.87$ for late May and early June the instantaneous growth rate progressively fell to a low of $g_w = 1.28$ for late March to early April. During late April to early May of the ultimate year, $g_w = 1.74$. The instantaneous growth rate then fell to $g_w = 1.14$ during mid July to early August. It was concluded that growth, in length and weight, of central British Columbia pink salmon is a continuing process with no period of complete cessation from the time the fry enter the sea until the time they re-enter the estuary as adults.

INTRODUCTION

Along the coast of central British Columbia (Fig. 1), pink salmon (*Oncorhynchus gorbuscha*) fry enter the sea principally during April and May. After a brief period of residence in the inlets and enclosed waters, the juveniles migrate offshore into the open ocean. The following year, in July and August, the fish again appear in the coastal and enclosed waters as maturing adults. While it is generally known that pink fry enter the sea at about 3.5 cm fork length (0.2 g live weight) and are at return 40–60 cm long (1.5–2.5 kg in weight), little has been presented in the literature concerning their specific growth rates during the intervening 15–17 months.

It is the purpose of this communication to present and analyse data now available on marine growth rates of pink salmon and to compare the results with information reported from other areas.

[1]Received for publication April 21, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

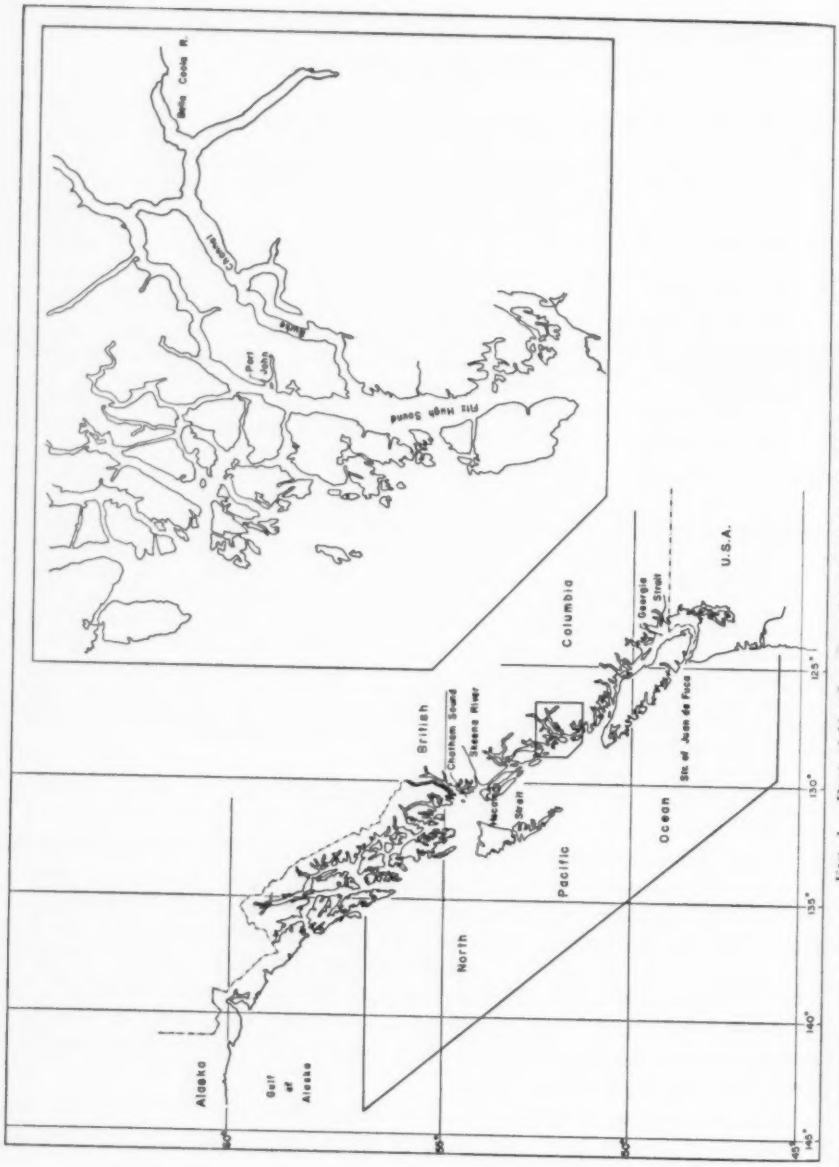


FIG. 1. Part of Northeastern Pacific Ocean showing areas covered in report.

METHODS AND MATERIALS

Data on growth of pink salmon were obtained as a by-product of several studies which had other objectives. Samples of fish were obtained from high seas tagging programs carried out in the North Pacific in 1962 and 1963 to determine salmon distribution (INPFC Ann. Rept. for 1962 and 1963). Size data for juvenile salmon were provided through various studies undertaken in 1956 (INPFC Ann. Rept. for 1956), and in 1961 to 1963, on early sea life, distribution, and natural mortality of salmon. Most of the oceanic samples were obtained using Japanese long-line gear and in one instance a mid-water trawl was employed. The juveniles were captured by small seines operated from skiffs or low-powered vessels.

Two approaches will be used in providing size-at-time data from which instantaneous growth rates can be deduced. The first approach uses length–frequency data obtained from samples drawn at different times in the same or different areas. The second method uses the measured increase in size of marked or tagged individuals. Both techniques present practical and theoretical difficulties which are dealt with in appropriate sections of the analysis.

Instantaneous growth rates in length are estimated from the relationship

$$g_l = \frac{\mathrm{Ln}\, l_t - \mathrm{Ln}\, l_o}{t} \tag{1}$$

where g_l denotes the instantaneous growth rate in length during the time period t, and is, in this text, on a per-day basis. The symbol l denotes fork length in centimetres. The abbreviation Ln denotes the natural logarithm ($\log_e$) of the specified term. For a particular period of life history g_l may be estimated as the slope of a regression line fitted (either mathematically or by eye) to $\mathrm{Ln}\, l = f(t)$ data. Assuming the length–weight expression

$$w = al^b \tag{2}$$

to apply, the instantaneous growth rate in weight is obtained by the relationship

$$g_w = bg_l. \tag{3}$$

Here g_w denotes the instantaneous growth rate in weight, b is the slope constant, and a the intercept of equation (2) in log form.

Length measurements were taken from fish preserved in formalin, from fish held frozen, from fish measured alive either with or without anaesthesia, and from fresh dead specimens. It is fairly well established that length measurements taken from fish relaxed by anaesthesia average longer than those taken from normal live fish (Hartt, 1962). Fish measured alive without anaesthesia average shorter than the same fish measured dead in fresh condition (Parker, 1962, 1963a). Fish measured alive under anaesthesia also shrink when killed and preserved in formalin (see Parker, 1963b, for summary). Fresh dead fish were found to be longer than specimens frozen, thawed, and remeasured, (LeBrasseur and Barner, MS, 1964). To compensate for these effects, lengths

TABLE I. Percentage length–frequency data of East Fisher Channel pink salmon samples, April 18–25, 1961.
For identification of sample numbers see Fig. 2.

Group (*cm*)	Group value (central) (Ln *l*)	Sample number 1	2	3	4	5	6	7	8	9	10	11
		April 18	19	19	19	19	20	20	20	24	25	25
2.8–3.0	1.05	1.6	...	...	...	...	0.8	...	...	0.4	...	...
3.1–3.3	1.15	21.9	15.5	1.7	0.7	1.4	10.0	6.0	9.6	6.3	3.9	...
3.4–3.6	1.25	63.9	49.7	21.0	17.6	30.6	60.1	35.6	39.6	27.9	11.2	3.0
3.7–4.0	1.35	12.6	21.9	35.3	45.6	16.3	24.1	31.9	34.2	42.2	32.1	15.2
4.1–4.4	1.45	...	11.3	42.0	30.6	41.9	4.2	24.7	15.6	11.6	23.9	21.7
4.5–4.9	1.55	...	1.6	...	5.5	7.7	0.8	1.2	0.5	11.2	22.9	45.8
5.0–5.4	1.65	...	...	...	...	0.7	...	0.6	0.5	0.4	6.0	11.3
5.5–6.0	1.75	...	...	...	...	0.7	...	...	...	...	...	3.0
6.1–6.6	1.85	...	...	...	...	0.7	...	...	...	...	...	...
Totals (per cent)		100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Sample size		64	123	119	147	141	120	166	219	258	231	203

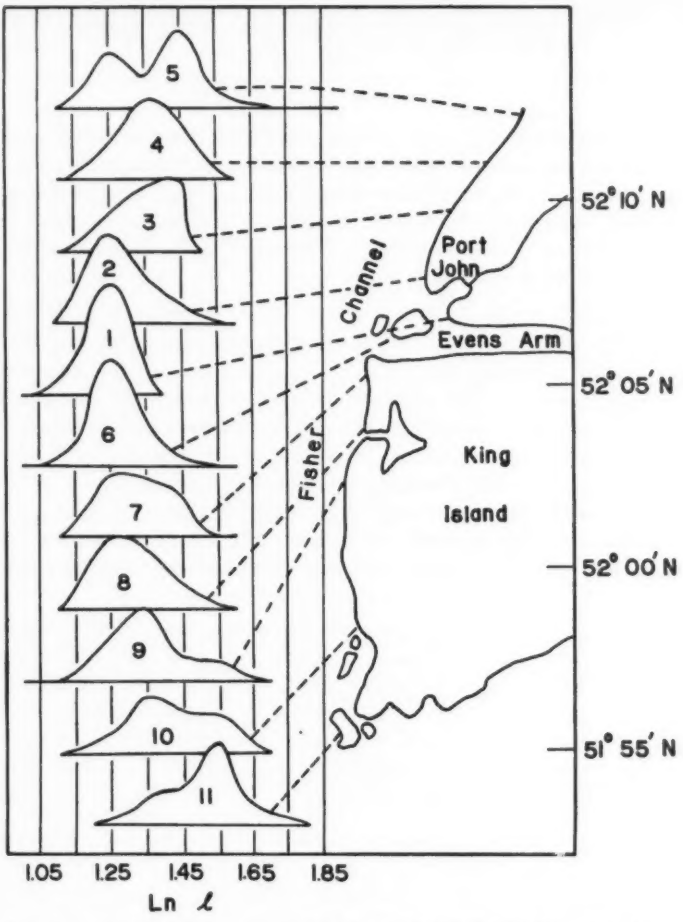


FIG. 2. Length–frequency curves associated with samples taken away from mark release area, Port John 1961, from Table I.

taken from anaesthetized live and from fresh dead fish were first adjusted to approximate live unanaesthetized measurements by multiplication by 0.95. Formalin-preserved and frozen specimens were assumed to provide this measurement without correction. Lengths were then grouped by 0.1 units of Ln *l*.

Fry and fingerling weights were taken after transporting the samples alive to a weighing station on shore. Weight was approximated to 0.01 g on anaesthetized fish. At sea, weights of freshly killed salmon were approximated to the nearest 0.1 lb (0.045 kg). Length–weight relationships were computed from these data and apply to whole weights including the stomach and its contents. There are undoubtedly differences in weight of fish due to the method of pre-

servation but conversion factors are unavailable. However, it is not likely that a general weight–length relationship will suffer from the lack of more precise measurement.

GROWTH IN LENGTH

From April into June, in each of the years 1961, 1962, and 1963, populations of juvenile pink salmon were extensively sampled in the Fitz Hugh Sound area of central British Columbia. From these samples, length frequency curves were plotted which, in general, reflect the growth of pink salmon during the period of coastal residence. Caution must be exercised in the interpretation of these data for the following reasons.

1. Entrance into the sea mainly occurs over a 4–6-week period. Fry quickly form schools which tend to follow the shoreline dispersing the population away from the estuary. During the period of fry entrance into the sea, growth proceeds at a rapid rate so that samples obtained farthest from the source stream generally contain larger individuals than those obtained near the estuary. This feature is demonstrated by length–frequency data presented in Table I. The progressive increase in size moving away from the marking site is shown in Fig. 2 which depicts length frequencies as equal area curves for samples taken in various areas. Samples generally contained more than 100 fish of which 5–20% had marks and could thus be identified as having originated at Port John (Parker, 1964).

2. A further complication arises in conjunction with a behavioural change which appears to be linked with size. As fish grow to 4.5–5.5 cm they maintain their schooling habit but move farther away from the shoreline. This leads to a non-random size distribution within the larger schools and accumulations. Larger fish are found in the part of the school farthest from the shore and vice versa. This feature is demonstrated by comparison of two length–frequency distributions presented in Table II and Fig. 3. Both samples were taken from

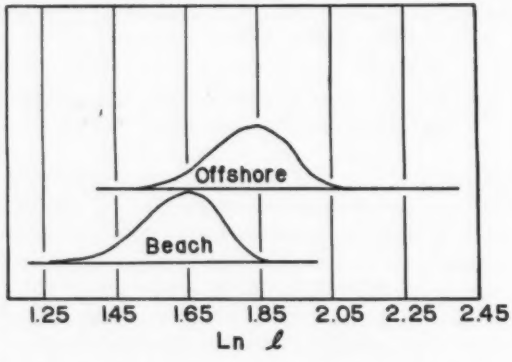


FIG. 3. Length–frequency curves for beach and offshore samples taken from the same accumulation, Fitz Hugh Sound, British Columbia, May 17, 1962, from Table II.

TABLE II. Percentage length–frequency data obtained from a single accumulation of pink salmon fingerling, Fitz Hugh Sound, May 17, 1962.

Group (*cm*)	Grand value (central) (Ln *l*)	Sample location	
		Beach	Offshore
3.4– 3.6	1.25	0.6	...
3.7– 4.0	1.35	2.8	...
4.1– 4.4	1.45	8.7	1.3
4.5– 4.9	1.55	26.4	0.7
5.0– 5.4	1.65	38.6	9.8
5.5– 6.0	1.75	21.3	25.4
6.1– 6.6	1.85	0.8	35.1
6.7– 7.3	1.95	0.8	20.3
7.4– 8.1	2.05	...	6.0
8.2– 9.0	2.15	...	0.7
9.1– 9.9	2.25	...	0
10.0–11.0	2.35	...	0.7
Totals		100.0	100.0
Sample size		508	153

the same accumulation. The sample containing the smaller fish was obtained within 10 m of the shore while the sample containing the larger individuals was taken about 30 m farther offshore. This is neither an isolated nor an unusual feature of size distribution of pink salmon juveniles; rather it is typical of the non-random size distribution existing within the coastal area.

Despite these non-random distributions, estimates of size are probably reasonably representative. Sampling throughout the inshore area was extensive and thorough. The length–frequencies obtained indicate the range of sizes of fish present within the area during stated time intervals. No quantitative data are available with which to weight the size data into population estimates. For lack of weighting data, each sample was given equal weight by converting to a percentage basis. Within time periods, these samples were then combined and the resulting frequencies again reduced to a percentage basis. The resulting length–frequency distributions for 1961, 1962, and 1963 are presented in Tables III–V and graphically shown as equal area curves in Fig. 4–6. The regression of Ln l on time (days) was computed from data in Tables III–V and the regression lines are shown in Fig. 4–6 as solid lines, which fit the series fairly well, thus suggesting exponential growth. The slopes (g_l) of these regressions are: 1961, 0.0158; 1962, 0.0150; 1963, 0.0146 natural log units per day.

Emigration of pink salmon fingerling from the enclosed waters of Fitz Hugh Sound occurred during late May and early June. Again, this movement reflects a behavioural change and occurs when the bulk of the population reaches 6–8 cm. It is suspected that emigration of the larger fish takes place prior to that of the

TABLE III. Percentage length–frequency data of 1961 juvenile pink salmon, Fitz Hugh Sound, British Columbia.

Group (*cm*)	Group value (central) (Ln *l*)	April		May					June
		19	25	1	8	15	27	29	6
2.8– 3.0	1.05	0.3	0.1	...	...	...	...	...	...
3.1– 3.3	1.15	8.2	3.3	0.3	0.1	...	...	...	...
3.4– 3.6	1.25	39.8	19.1	4.5	1.1	...	...	...	...
3.7– 4.0	1.35	26.8	35.0	23.9	7.8	0.2	...	...	...
4.1– 4.4	1.45	22.1	18.1	35.5	15.8	1.1	...	...	...
4.5– 4.9	1.55	2.4	19.0	20.3	35.8	4.9	...	...	...
5.0– 5.4	1.65	0.2	4.4	11.7	26.5	19.1	1.9	...	0.4
5.5– 6.0	1.75	0.1	0.7	3.8	9.4	34.7	24.1	0.8	1.1
6.1– 6.6	1.85	0.1	0.2	...	2.7	31.8	43.4	0.8	18.1
6.7– 7.3	1.95	...	0.1	...	0.6	8.0	26.3	7.5	59.6
7.4– 8.1	2.05	...	...	...	0.2	0.2	4.3	34.9	20.0
8.2– 9.0	2.15	...	...	...	...	...	...	41.9	0.8
9.1– 9.9	2.25	...	...	...	...	...	...	10.9	...
10.0–11.0	2.35	...	...	...	...	...	...	2.4	...
11.0–12.1	2.45	...	...	...	...	...	...	0.8	...
Totals (per cent)		100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Number of samples		6	7	6	8	4	3	1	1
Numbers of fish		879	1409	1250	1481	406	695	118	266

TABLE IV. Percentage length–frequency data of 1962 juvenile pink salmon, Fitz Hugh Sound, British Columbia.

Group (*cm*)	Group value (central) (Ln *l*)	April	May					June
		28	3	8	13	19	25	31	11
2.8– 3.0	1.05	...	0.1	...	...	...	...	...	...
3.1– 3.3	1.15	0.6	2.3	0.5	2.2	0.1	...	...	...
3.4– 3.6	1.25	10.5	33.2	9.7	10.3	0.7	...	...	...
3.7– 4.0	1.35	48.8	31.3	20.4	19.0	5.5	1.1	...	...
4.1– 4.4	1.45	33.3	14.3	15.9	19.5	7.1	5.9	0.1	...
4.5– 4.9	1.55	5.6	11.6	20.9	20.4	12.1	9.8	1.7	...
5.0– 5.4	1.65	1.0	5.7	15.5	17.5	18.2	23.8	8.7	...
5.5– 6.0	1.75	0.2	1.4	12.4	6.6	33.0	31.2	28.0	...
6.1– 6.6	1.85	...	0.1	3.9	4.5	15.2	23.8	31.8	5.0
6.7– 7.3	1.95	...	...	0.7	...	6.6	3.8	25.6	40.2
7.4– 8.1	2.05	...	...	0	...	1.3	0.5	3.7	49.7
8.2– 9.0	2.15	...	...	0.1	...	0.1	0.1	0.4	5.0
9.1– 9.9	2.25	...	...	...	...	0	...	...	0.1
10.0–11.0	2.35	...	...	...	...	0.1	...	...	...
Totals (per cent)		100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Number of samples		3	2	5	3	10	5	7	4
Numbers of fish		1217	886	1438	988	5088	2661	2744	1237

TABLE V. Percentage length–frequency data of 1963 juvenile pink salmon, Fitz Hugh Sound, British Columbia.

Group (*cm*)	Group value (central) (Ln *l*)	April			May						June
		18	25	30	4	8	16	22	25	29	5
2.8– 3.0	1.05	...	...	0.5	...	...	...	...	...	...	...
3.1– 3.3	1.15	3.3	1.8	13.1	0.2	...	...	...	...	...	...
3.4– 3.6	1.25	16.5	14.7	27.2	1.7	0.3	...	...	...	...	...
3.7– 4.0	1.35	12.3	24.0	21.9	13.3	2.8	...	...	...	...	...
4.1– 4.4	1.45	11.2	12.6	14.4	25.0	7.5	0.1	0.8	...	...	...
4.5– 4.9	1.55	30.5	6.9	9.4	29.5	14.8	2.1	9.0	1.4	...	...
5.0– 5.4	1.65	19.3	13.2	5.3	11.8	15.5	11.5	23.0	11.0	...	...
5.5– 6.0	1.75	5.8	13.9	5.8	9.5	13.6	21.0	27.8	24.7	...	0.2
6.1– 6.6	1.85	1.0	7.6	1.7	7.3	16.2	12.9	20.0	24.7	0.9	5.5
6.7– 7.3	1.95	0.1	4.5	0.6	1.7	19.1	19.2	12.6	20.2	7.5	29.5
7.4– 8.1	2.05	...	0.6	0.1	...	7.8	24.7	6.0	13.3	47.6	20.4
8.2– 9.0	2.15	...	0.2	...	...	2.3	6.7	0.8	3.9	39.4	20.2
9.1– 9.9	2.25	...	...	...	...	0.1	1.8	...	0.8	4.2	18.9
10.0–11.0	2.35	...	...	...	...	...	...	...	...	0.4	4.5
11.1–12.1	2.45	...	...	...	...	...	...	...	...	...	0.8
Totals (per cent)		100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Number of samples		8	5	18	7	16	3	2	2	1	2
Numbers of fish		1999	2106	11236	2230	6470	1095	746	499	223	499

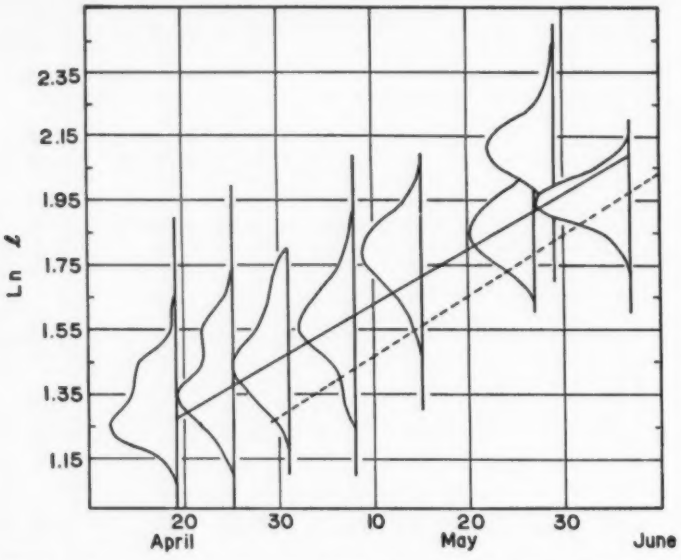


FIG. 4. Length–frequency curves of 1961 juvenile pink salmon, Fitz Hugh Sound, British Columbia, from Table III (see text for explanation).

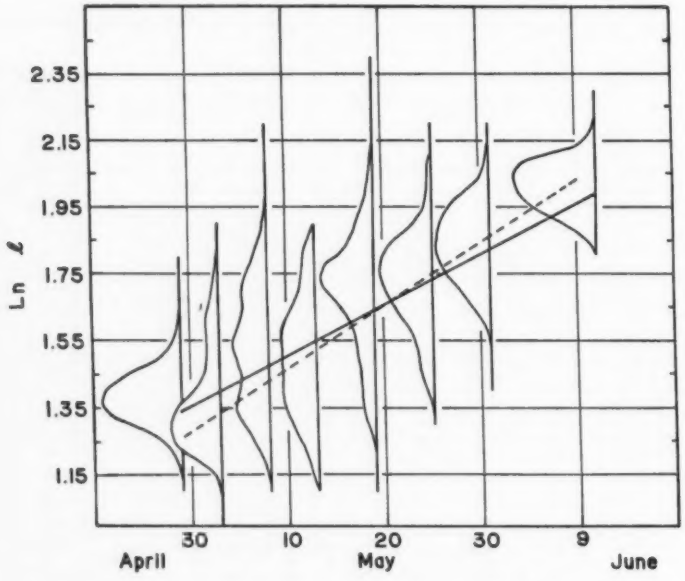


FIG. 5. Length–frequency curves of 1962 juvenile pink salmon, Fitz Hugh Sound, British Columbia, from Table IV (see text for explanation).

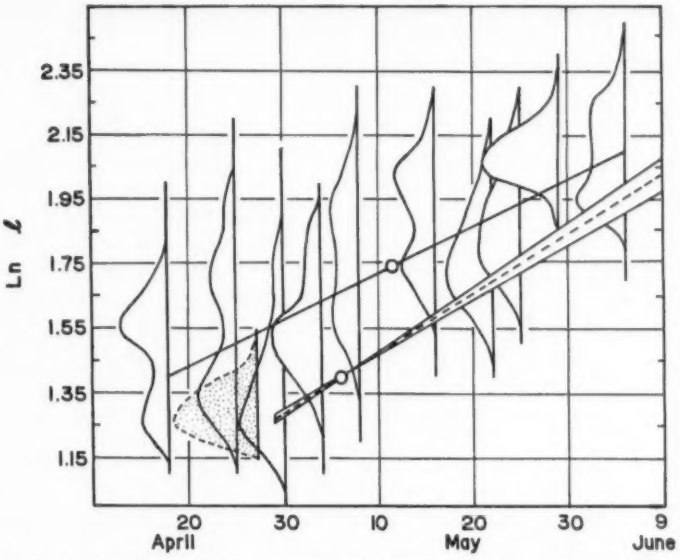


FIG. 6. Length–frequency curves of 1963 juvenile pink salmon, Fitz Hugh Sound, British Columbia, from Table V and VI (see text for explanation).

main population. This may be deduced from a study of Fig. 4–6 where it may be seen that larger fish encountered early in the season are not usually found at an advanced size (assuming similar growth rates for large and small fingerling) in late May and June. With entrance of fry of a uniform size over a protracted period, and emigration of the larger fingerling prior to the general population movement, growth rates estimated by average size in time data will be less than the actual average growth rate. Therefore, the growth rates indicated by the above regression analysis are probably too small.

In 1963, a total of 170,000 pink salmon fry was marked in the estuary of the Bella Coola River and released on April 28. Subsequent sampling of the fry in the Burke Channel–Fitz Hugh Sound area gave the opportunity to re-measure 154 of these individuals during the time period April 29 to June 9. These data are presented in Table VI. Again assuming exponential growth, the regression of Ln $l = f(t)$ yields a slope (g_l) of 0.0186 with 0.95 confidence interval of 0.017 to 0.020. This regression line and the confidence intervals on the slope are plotted in Fig. 6 as a dashed line enclosed within two solid lines. The length–frequency curve of the original marked population released is indicated by the shaded area. The instantaneous growth rate is not likely to be constant but will decelerate with increase in size, therefore the assumption of exponential growth will tend to underestimate the instantaneous growth rate during the initial portion and overestimate it during the later portions of the time period. Furthermore, it is likely that marking will tend to reduce rather than enhance a fish's growth opportunities. It is also possible that the fastest-growing marked

TABLE VI. Percentage length–frequency data on growth of marked fish released April 28, 1963, Bella Coola River estuary, British Columbia.

Group (*cm*)	Group value (central) (Ln *l*)	April 27 marked sample (*per cent*)	April		May										June		
			29	30	1	3	4	8	9	10	22	24	30	31	1	8	9
3.1–3.3	1.15	5.6	16	..	2	..	..	..	..	..	..	..	..	..	..	..	..
3.4–3.6	1.25	52.3	50	5	10	..	..	..	..	..	..	..	..	..	..	..	..
3.7–4.0	1.35	39.6	21	3	5	1	6	2	..	..	..	..	..	..	..	..	..
4.1–4.4	1.45	2.4	..	..	1	..	1	3	..	1	..	..	..	..	..	..	..
4.5–4.9	1.55	0.1	..	..	..	1	..	1	1	..	..	..	..	..	..	..	..
5.0–5.4	1.65	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
5.5–6.0	1.75	..	..	..	..	..	..	..	..	..	..	1	1	..	..	..	..
6.1–6.6	1.85	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..
6.7–7.3	1.95	..	..	..	..	..	..	..	..	..	..	..	..	1	2	..	1
7.4–8.1	2.05	..	..	..	..	..	..	..	..	..	..	..	..	..	2	4	8
8.2–9.0	2.15	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3
Totals		100.0	87	8	18	2	7	6	1	1	1	1	1	1	4	4	12
Days (+)		0	1	2	3	5	6	10	11	12	24	26	32	33	34	41	42

TABLE VII. Percentage length–frequency data for 1956 juvenile pink salmon, Chatham Sound, British Columbia.

Group (*cm*)	Group value (central) (Ln *l*)	July				August		Sept.
		11	16	23	31	12	25	6
3.1– 3.3	1.15	0.2	...	...	...	...	...	...
3.4– 3.6	1.25	0.2	...	...	...	...	...	...
3.7– 4.0	1.35	0	...	...	...	...	...	...
4.1– 4.4	1.45	0	...	...	...	...	...	...
4.5– 4.9	1.55	0.2	...	...	0.1	...	...	...
5.0– 5.4	1.65	3.1	...	...	0.3	...	...	...
5.5– 6.0	1.75	6.9	...	...	0.3	...	...	...
6.1– 6.6	1.85	30.6	...	...	1.9	...	...	...
6.7– 7.3	1.95	32.4	3.2	...	4.8	...	...	...
7.4– 8.1	2.05	14.8	29.0	...	6.2	...	...	...
8.2– 9.0	2.15	11.3	39.4	52.7	33.2	0.9	...	...
9.1– 9.9	2.25	0	23.3	41.3	43.9	13.7	...	...
10.0–11.0	2.35	0	3.8	6.0	9.0	26.1	...	0.3
11.1–12.1	2.45	0	1.3	...	0.3	30.5	4.9	1.4
12.2–13.4	2.55	0	...	...	...	23.3	42.9	6.0
13.5–14.8	2.65	0.3	...	...	...	4.6	38.9	50.6
14.9–16.4	2.75	...	...	...	...	0.9	13.3	35.0
16.5–18.1	2.85	...	...	...	...	...	...	5.7
18.2–20.0	2.95	...	...	...	...	...	...	0.5
20.1–22.1	3.05	...	...	...	...	...	...	0.5
Totals (per cent)		100.0	100.0	100.0	100.0	100.0	100.0	100.0
Number of samples		5	7	2	11	7	5	12
Numbers of fish		253	139	43	811	279	136	255

TABLE VIII. Percentage length–frequency data for November 1963 juvenile pink salmon, Hecate Strait, British Columbia.

Group (*cm*)	Group value (central) (Ln *l*)	November 8
14.9–16.4	2.75	0.8
16.5–18.1	2.85	15.8
18.2–20.0	2.95	48.1
20.1–22.1	3.05	24.8
22.2–24.5	3.15	9.0
24.6–27.1	3.25	1.5
Total (per cent)		100.0
Number of fish		257

TABLE IX. Percentage length–frequency data for January 1963 juvenile pink salmon, northeastern Pacific Ocean.

Group (*cm*)	Group value (central) (Ln *l*)	January 28
24.6–27.1	3.25	27.3
27.2–29.9	3.35	27.3
30.0–33.1	3.45	36.4
33.2–36.5	3.55	9.0
Total (per cent)		100.0
Number of fish		11

fish had left the sampling areas during the sampling period leaving only the slower-growing individuals susceptible to recapture. For these reasons $g_l = 0.0186 \pm 0.0015$ may be too low.

The growth regression line derived from the marked population is also plotted as dashed lines in Fig. 4 and 5. Additional comparisons of the 1961, 1962, and 1963 juvenile pink salmon populations may be made from a consideration of these figures. The time of entrance and residence in the enclosed waters of the 1962 population was about 10 days later than in 1961. The 1963 population contains both early and late elements as disclosed by its persistent bimodal length–frequency curves. There is no indication that fish grew at different rates among the years studied, in fact in all three years the advance in size of the smallest length–frequency groups compares well with the regression line computed from the marked population. It is suggested that growth rates were similar during the three years while occurring during slightly different calendar time periods. The best estimate of the instantaneous growth rate in length on a 30-day basis for the initial marine period of central British Columbia pink salmon is, then, 30 $g_l = 0.559$ (30 days at the daily rate $g_l = 0.0186$ calculated above).

Seining from the beaches and over deep water during July, August, and early September in Chatham Sound in 1956 produced catches of juvenile pink salmon. Length–frequency data for these samples are presented in Table VII. In November 1963, catches of juvenile pink salmon were made in northern Hecate Strait within 10 miles of shore with a midwater trawl. Length–frequency data for these samples are presented in Table VIII. Exploratory fishing in the Gulf of Alaska during late January 1963 along a track between Vancouver Island and Kodiak Island, Alaska, produced a total of 11 pinks. Length–frequency data for this sample are presented in Table IX.

Tagging operations in the northeastern Pacific in 1962 were carried out from April to July from the B.C. coastline to 160° W longitude using surface long-line gear. Alive and undamaged fish were measured to the nearest 0.5 cm, tagged with Petersen disc tags and released. Lengths and weights were taken from sampled fish unfit for tagging. In total, 8911 pink salmon were caught and 7929 tagged and released; of the latter 538 or 6.8% were recovered.

Tagging was again carried out in the northeastern Pacific during April and May 1963. During this period, 2668 pink salmon were caught of which 2175 were tagged and released. Reliable lengths and weights were obtained, using beam balances, from fish retained from the catches. In total, 30 of these 1963 releases have been recovered to date.

From the pattern of recoveries in 1962 it was recognized that returns to central British Columbia were consistently from within an area extending to about 300 miles offshore. Furthermore, until July there were few tag recoveries from this area to coastal regions other than central British Columbia. The oceanic area approximately encompassing central British Columbia pink salmon is enclosed by the line running parallel to the coast shown in Fig. 1. Length–frequency data of catches within this area during 1962 are presented in Table X.

TABLE X. Percentage length–frequency data for 1962 oceanic pink salmon catches for British Columbia area as shown in Fig. 1.

Group (*cm*)	Group value (central) (Ln *l*)	April		May	June		July	
		15	29	15	3	20	8	20
22.2–24.5	3.15	0.5	...	...	...	...	...	...
24.6–27.1	3.25	1.0	...	0.2	...	...	...	...
27.2–29.9	3.35	28.7	...	0	...	...	...	...
30.0–33.1	3.45	38.8	2.3	0.6	...	0.1	...	...
33.2–36.5	3.55	22.9	13.0	1.1	0.4	0.5	...	...
36.6–40.3	3.65	5.6	47.0	25.2	10.4	1.4	0.5	...
40.4–44.6	3.75	2.0	26.3	48.2	60.8	23.9	6.2	4.2
44.7–49.3	3.85	0.5	10.2	18.9	26.0	64.7	58.4	48.5
49.4–54.5	3.95	...	0	4.5	2.2	8.3	30.4	40.9
54.6–60.2	4.05	...	1.2	1.3	0.2	1.1	4.4	6.1
60.3–66.5	4.15	...	...	...	...	...	0.1	0.3
Totals (per cent)		100.0	100.0	100.0	100.0	100.0	100.0	100.0
Numbers of fish		192	177	423	945	757	1532	624

The length–frequency data for the entire eastern Pacific oceanic catch of pink salmon taken by Fisheries Research Board exploratory vessels in 1963 are presented in Table XI.

Samples of pink salmon taken offshore were found to contain approximately equal portions of males and females. Shore samples taken in central British Columbia during 1962, in contrast, show a preponderance of males early and late in the run (2:1), but during mid season, females were more abundant in the catches than males. The oceanic length–frequency data do not differentiate between the sexes. Because it is necessary to present the coastal commercial catches in a comparable manner, length–frequency data obtained from commercial purse seine catches in the central British Columbia area (presumably non-selective for length) were grouped by sex and then weighted to simulate an equal

sex ratio. These length–frequency data, representative of central British Columbia pink populations in 1962, are presented in Table XII.

Length–frequency curves for the 1961 and 1962 Fitz Hugh Sound juveniles (Tables III and IV), 1956 Chatham Sound juveniles (Table VII), November and January 1963 samples (Tables VIII and IX), 1962 and 1963 oceanic samples (Tables X and XI), and the 1962 central British Columbia catch (Table XII) are presented in Fig. 7. For the early stages (Fitz Hugh Sound data) April 20 is taken as the central date of entrance of fry into the sea. Most fry fall within

TABLE XI. Percentage length–frequency data for 1963 eastern Pacific oceanic pink salmon catches.

Group (*cm*)	Group value (central) (Ln *l*)	April			May		
		9	20	30	11	22	31
20.1–22.1	3.05	0.5	...	...	...	...	...
22.2–24.5	3.15	0	...	...	...	...	...
24.6–27.1	3.25	0.5	...	...	...	...	...
27.2–29.9	3.35	4.5	...	...	...	...	...
30.0–33.1	3.45	34.7	24.5	4.2	1.2	0.2	...
33.2–36.5	3.55	33.5	49.1	36.2	16.8	6.1	0.4
36.6–40.3	3.65	17.3	17.9	23.7	51.2	49.1	34.3
40.4–44.6	3.75	7.3	5.7	25.2	24.4	37.1	54.3
44.7–49.3	3.85	1.7	1.9	8.0	5.6	6.1	10.1
49.4–54.5	3.95	...	0.9	1.9	0.8	1.2	0.9
54.6–60.2	4.05	...	...	0.8	...	0.2	...
60.3–66.5	4.15	...	...	...	...	...	...
Totals (per cent)		100.0	100.0	100.0	100.0	100.0	100.0
Numbers of fish		179	106	262	250	604	702

TABLE XII. Percentage length–frequency data for central British Columbia maturing pink salmon, 1962, from commercial seine catch (weighted to equal sex ratio).

Group (*cm*)	Group value (central) (Ln *l*)	July		August			
		19	28	1	8	14	23
36.6–40.3	3.65	12.0	...	...	5.3	...	2.6
40.4–44.6	3.75	16.0	10.0	4.0	4.0	4.0	47.4
44.7–49.3	3.85	26.0	54.0	34.0	41.4	30.0	42.1
49.4–54.5	3.95	30.0	26.0	36.0	33.3	48.0	7.9
54.6–60.2	4.05	16.0	8.0	22.0	14.7	12.0	...
60.3–66.5	4.15	...	2.0	4.0	1.3	6.0	...
Totals (per cent)		100.0	100.0	100.0	100.0	100.0	100.0
Numbers of fish		50	50	50	75	50	38

the size group 3.4–3.6 cm. The central Ln l value for this group is 1.25. For the first 30-day period a g_l value of 0.559, calculated from the marked fry, is used, producing the line shown in Fig. 7. Growth during this period (Fig. 4–6 and Table VI) is approximately exponential.

From the Ln l value of 1.809 at May 20 to 3.950 at August 10 of the following year, a total instantaneous growth rate of 2.141 applies for the 450-day time-period. The distribution of growth rate within this time-period can be interpreted from the length–frequency curves. In general, growth appears to proceed throughout the 450-day period at a gradually decreasing rate. There are, however, two points of interpretation that must be examined. The first is associated with Chatham Sound samples. The first four length–frequencies lie a considerable distance below a general growth curve. These samples were primarily taken from beach accumulations and may represent only the smaller sizes present in the area. Their location suggests that they may have been Skeena River fish which entered the marine environment much later (20–30 days) than the Fitz Hugh Sound populations. Whatever the basis for difference, they do not fit a general pattern of growth rate encompassing the three later Chatham Sound samples with data obtained earlier (Fitz Hugh Sound) and later (Hecate Strait, November 1963).

The second point requiring interpretation is the apparent inflection in April of the ultimate year suggesting an increase in growth rate associated with the end of the biological winter in the sea. This is shown by the large samples of pink salmon in their ultimate year taken during April of both 1962 and 1963. The exact location of this inflection is in doubt, for the preceding time-period is represented by only a single small sample (11 fish) taken in January 1963 and prior to that, a fairly large sample (252 pink) taken in November 1963, but in inshore waters and with a different type of gear (midwater trawl). It is equally possible to interpret these data as showing an inflection much earlier, perhaps as January or February. Indeed, this is the conclusion reached by Birman (1960) for East Kamchatka pink salmon. No further arguments can be advanced without acquiring more evidence. However, these data appear to support conclusively the contention that an inflection in the growth curve does indeed occur sometime between January and May.

The final length–frequency of the 1962 shore sample taken in late August represents fish noticeably smaller than the preceding sample. This sample cannot be included in any trend line of growth rate for negative growth in length, to that degree, is not acceptable. Rather, this sample may reflect either sampling error or a population of small individuals which assumes relative importance at the end of the salmon run.

With these interpretations three smooth curves have been drawn by eye through the length–frequency distributions as shown in Fig. 7. The general pattern of growth, as interpreted by these curves has the following characteristics. An initial period (40 days) of fast growth (30 g_l = 0.559) is terminated by a rapid change in growth rate coinciding with the exodus of the population from the enclosed waters. During a second growth stanza (270 days) the instan-

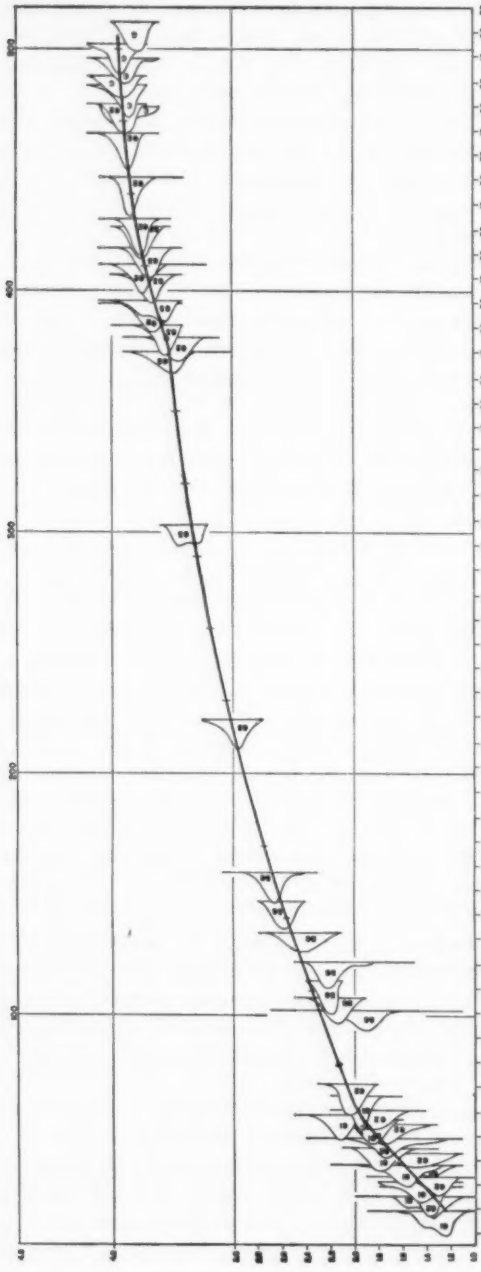


FIG. 7. Growth rate of central British Columbia pink salmon as interpreted in text. The "y" axis is scaled in units of Ln fork length. Figures within the curves indicate year of sampling, *c* denotes 1962 samples from commercial catch.

TABLE XIII. Schedule of estimated instantaneous growth rates in length for British Columbia pink salmon from Fig. 7.

Time period (*days*)	Ln *l*	ΔLn *l* (g_l per 30 day)	Life history stage
0[a]	1.250		Entrance into sea
		0.559	
30	1.809		
		0.324	Departure from inshore waters
60	2.133		
		0.226	
90	2.359		
		0.203	
120	2.562		
		0.192	
150	2.754		
		0.169	
180	2.923		
		0.147	
210	3.070		
		0.127	
240	3.197		
		0.113	
270	3.310		
		0.094	
300	3.404	0.076	Biological winter
		0.077	
330	3.480		
		0.171	Spring
360	3.557		
		0.110	
390	3.728		
		0.071	
420	3.838	.	
		.	
450	3.909	0.041	Return to inshore waters and entry into fishery
480	3.950		

[a]April 20.

taneous growth rate regularly diminishes from 0.226 to 0.076 per 30-day period. Abruptly, about April 15, 30 g_l increases to 0.171, but again falls regularly to a value of 0.041 at the close of the marine period. A schedule of instantaneous growth rates, estimated from the curves in Fig. 7, is presented in Table XIII. It is noteworthy that these data indicate appreciable growth until the close of the period of marine life when the population enters fresh water.

GROWTH OF TAG RECOVERIES

Of the pink salmon tagged in 1962, 49 recoveries were reported from British Columbia and Southeastern Alaska with length measurements taken at recovery. Of these, 26 were recovered during the time-period covered by the growth curve presented in Fig. 7. These data are presented in Table XIV. For each fish an "expected" length at recovery was calculated based on instantaneous growth rates measured from the growth curve for fish free for an identical calendar period. These expected lengths and the deviations of observed from expected

are presented in Table XIV. The average of these deviations is +0.02 cm indicating that under the assumption of normal distribution of measurement error the information from tagging confirms the growth rates estimated from the length–frequency curves during the final 120 days at sea. In these data there is no indication that the tags depressed growth rate.

TABLE XIV. Comparison of growth of tagged pink salmon with "expected" growth estimated from growth curve in Fig. 7.

Date tagged	Length at Release (*cm*)	Length at Recovery (*cm*)	Time free (*days*)	g_1 from curve (Fig. 7)	"Expected" length (*cm*)	Deviations (expected–observed)
April 11	35.0	44.4	102	0.289	46.7	+2.3
May 16	44.5	50.0	70	0.138	51.1	+1.1
May 18	41.5	43.2	69	0.132	47.4	+4.2
May 29	43.0	53.3	70	0.107	47.9	−5.4
June 9	47.0	55.9	51	0.073	50.6	−5.3
June 10	36.5	38.1	42	0.066	39.0	+0.9
June 19	52.0	58.4	29	0.041	54.2	−4.2
June 19	54.0	54.8	50	0.058	57.2	+2.4
June 19	47.5	50.8	37	0.049	49.9	−0.9
June 28	47.0	45.7	42	0.043	49.1	+3.4
July 4	45.0	50.8	28	0.028	46.3	−4.5
July 4	47.0	52.1	20	0.023	48.1	−4.0
July 8	48.2	48.3	8	0.010	48.7	+0.4
July 8	49.1	49.5	9	0.011	49.6	+0.1
July 9	47.0	44.0	16	0.016	47.8	+3.8
July 11	51.0	52.1	28	0.024	52.2	+0.1
July 12	51.0	52.0	5	0.006	51.3	−0.7
July 12	48.5	49.5	25	0.021	49.5	0
July 12	54.5	54.6	8	0.010	54.6	0
July 13	44.0	35.6	25	0.021	44.9	+9.3
July 14	47.4	48.2	23	0.019	48.3	+0.1
July 14	53.5	58.4	13	0.013	54.2	−0.2
July 14	43.7	48.3	17	0.015	44.4	−3.9
July 15	51.0	55.9	18	0.015	51.8	−4.1
July 15	51.5	56.4	25	0.020	52.5	−3.9
July 15	51.5	48.0	19	0.016	52.3	+4.3

LENGTH–WEIGHT RELATIONSHIP

Length–weight samples are available from Fitz Hugh Sound juveniles for both 1962 and 1963. These cover the period from first appearance in the sea until the offshore migration. Frozen samples were measured from the 1962 pelagic fishing in June and July. Shipboard lengths and weights taken with a beam balance were available from the 1963 offshore fishing in April and May.

Fresh-landed catches in June and July 1962 were obtained from central British Columbia. Frozen catches from January 1963 fishing in the Gulf of Alaska and from November 1963 Hecate Strait fishing were processed ashore and data made available. Average lengths and weights from these samples are presented in Table XV. These values were logged (base 10) and are plotted in Fig. 8. A linear regression line was fitted and is plotted in Fig. 8. The slope of this length–weight relationship is 3.25.

TABLE XV. Averaged sample lengths and weights for northeast Pacific pink salmon.

Sample		Number of fish	Sample average		Log_{10} average	
			Length (*cm*)	Weight (g)	Length	Weight
Fitz Hugh Sound						
1962	May 3	100	4.494	0.612	0.6526	$\bar{1}$.7868
	May 14	100	4.414	0.656	0.6448	$\bar{1}$.8169
	May 17	200	5.903	1.496	0.7711	0.1749
	May 24	100	6.472	1.838	0.8110	0.2643
	May 31	100	6.945	2.406	0.8417	0.3813
	June 7	100	7.041	2.603	0.8476	0.4155
	June 13	100	7.176	2.630	0.8559	0.4200
1963	April 21	100	3.726	0.305	0.5712	$\bar{1}$.4778
	April 30	100	4.437	0.617	0.6471	$\bar{1}$.7903
	May 1	100	4.657	0.747	0.6681	$\bar{1}$.8733
	May 4	100	5.698	1.340	0.7557	0.1271
	May 10	100	6.391	2.067	0.8056	0.3153
	May 23	800	7.341	3.396	0.8658	0.5310
	May 29	100	8.624	5.577	0.9357	0.7464
	June 5	100	9.687	7.904	0.9862	0.8978
	June 11	300	9.219	6.189	0.9647	0.7916
Hecate Strait						
1963	Nov. 8	240	20.18	84.05	1.3051	1.9245
Gulf of Alaska						
1962	June–July	169	43.28	914.4	1.6363	2.9611
1963	Jan. 28	11	29.27	207.2	1.4664	2.3164
	Apr.–May	565	45.24	1193.8	1.6555	3.0770
B. C. catch						
1962	July–Aug.	355	49.43	1808.1	1.6940	3.2574

GROWTH RATES IN WEIGHT

Instantaneous growth rates in length presented in Table XIII are multiplied by $b = 3.25$ to obtain instantaneous growth rates in weight (equation 3). These transformations are presented in Table XVI. The last column contains the decimal coefficients of increase applicable to each time-period. This series has

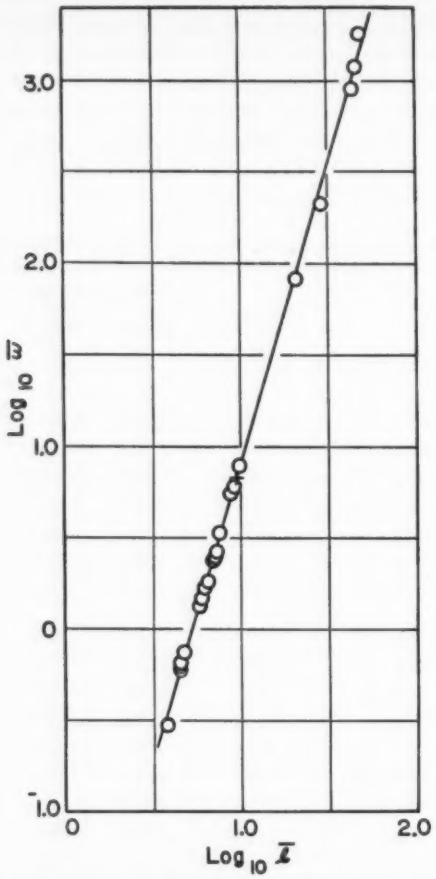


FIG. 8. Length–weight relationship for British Columbia pink salmon, from Table XVI.

several notable features, During the first 30-day period the fry increase in weight by a factor of 6.53. Growth during succeeding time-periods gradually slows, but even during February and March 28% increases in weight are estimated. This winter-growth period is followed by a spring increase of 74% during the 30-day period April 15 to May 15. Past this period, weight increase per 30-day period decreases to a value of 14% at which time the population has very nearly if not entirely approached or entered the natal stream.

DISCUSSION

The conclusions presented have been based upon samples of which some appear adequate while others lack numerical strength (i.e. the January 1963 Gulf of Alaska sample of 11 fish). All are subject to sampling error of one type

TABLE XVI. Instantaneous growth rates in weight (30-day basis) for central British Columbia pink salmon as calculated from Table XIII and equation (3).

Days	Time-period	g_t	g_w	e^{g_w}
0	April 20			
		0.559	1.817	6.53
30	May 20			
		0.324	1.053	2.87
60	June 19			
		0.226	0.734	2.08
90	July 19			
		0.203	0.660	1.93
120	August 18			
		0.192	0.624	1.87
150	September 17			
		0.169	0.549	1.73
180	October 17			
		0.147	0.478	1.61
210	November 16			
		0.127	0.413	1.51
240	December 16			
		0.113	0.367	1.44
270	January 15			
		0.094	0.306	1.36
300	February 14			
		0.076	0.247	1.28
330	March 16			
		0.077	0.250	1.28
360	April 15			
		0.171	0.556	1.74
390	May 15			
		0.110	0.358	1.43
420	June 14			
		0.071	0.231	1.26
450	July 14			
		0.041	0.133	1.14
480	August 13			

or another, particularly selectivity of gear used and non-random distribution of sizes in areas sampled. Samples representative of the fall and winter seasons are almost lacking; undoubtedly this void will be filled in the future and some of the above conclusions may have to be modified. Furthermore, since the growth rate is deduced from size-at-time data, it is the growth rate of the apparent population rather than of the surviving individuals which are described. It is possible that natural mortality may act differentially against the survival of the slower growing individuals of the population. Perhaps as distressing is the implicit assumption that a single stock has been sampled under a standard set of conditions. This requirement is only partly true for the ultimate-year spring and summer samples. It is almost certain not to be true of the Chatham Sound, Hecate Strait, and Gulf of Alaska 1963 samples. It is most nearly true of the Fitz Hugh Sound juvenile and commercial catch samples but even these contain some fraction of mixed stocks. Even and odd year races, genetically separate, have been combined. These may have different growth characteristics. Nevertheless the conclusions would not be greatly altered by selective elimination of some of these samples. The main conclusion which might be altered is that growth does not cease during the winter.

TABLE XVII. Length-at-time data for North Pacific pink salmon.

Dates	Areas	Average length (*cm*)	Source
May 29, 1906	Naha Bay	4.2	Chamberlain (1907)
June 18, 1906	Karluk	4.7	"
July 24, 1906	Karluk	7.7	"
July 24, 1906	Dundas Bay	8.0	"
May 18, 1948	Departure Bay, B.C.	4.0	Robertson (MS, 1948)
May 25, 1948	"	3.8	"
May 31, 1948	"	4.8	"
June 10, 1948	"	6.1	"
July 15, 1950	"	7.6	Foskett (1951)
June 15, 1955	Northern B.C.	6.5	Manzer (MS, 1955)
July 15, 1955	"	7.7	"
August 15, 1955	"	11.6	"
Early July 1956	"	7.7	Neave *et al.* (MS, 1956)
Late August 1956	"	15.0	"
Late May	E. Kamchatka	3.0	Birman (1960)
Sept. 19, 1959	"	21.0	"
End Sept. 1958	"	22.0	"
End Oct. 1959	S. Sakhalin	24.3	"
Mid Nov. 1959	"	25.6	"
December 1932	Primaria	26.6	"
End Dec. 1958	N.W. Pacific	28.0	"
Last Half Apr. 1959	"	41.0	"
End June 1959	Bering Sea	48.3	"
Early Sept. 1958	Gulf of Alaska	22.0	Hartt (1962)
June 14, 1957	S. of Aleutian Is.	42.8	"
June 8–20, 1957	"	43.7	"
June 6	"	44.1	"
May 27–June 17, 1957	"	47.3	"
June 7, 1959	"	44.3	"
June 4, 1959	"	46.8	"
May 22–29, 1960	"	43.2	"
June 7, 1960	"	42.2	"
Early May	Japanese land-based long-line fishery	40.5	Ishida (1963)
Mid May	"	42.9	"
Late May	"	43.1	"
Early June	"	43.6	"
Mid June	"	44.4	"
Late June	"	47.8	"

The existence of a break in the growth curve at a size of about 6–8 cm is not surprising. As outlined earlier, this is accompanied by a change in behaviour which results in a mass migration of the population out of the inlets. These changes are suggestive that a physiological change occurs at that size, similar to the parr–smolt transformation of other Pacific salmon.

A further question arises concerning the continued growth of the population during its re-entrance into coastal and enclosed waters. Along the coast of British Columbia the troll fishery, while actively fishing for chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*), takes many thousands of pink salmon each year. Actively-feeding pink salmon are also caught in inside waters both by trollers and sports fishermen in some areas, notably Johnstone Strait, Strait of Georgia, and Strait of Juan de Fuca. In the enclosed waters of Fitz Hugh Sound, purse-seine and gill-net fisheries are conducted from mid July to late August on pink salmon which generally are not feeding and presumably their growth has ceased. As seen in Fig. 7, the length of pink salmon taken in the commercial fishery samples increases throughout the season. This suggests that fish arriving late in the run had continued to feed in the coastal area and entered the enclosed waters later than the smaller earlier arrivals.

Several observations on size of pink salmon at different times are available in the literature and as unpublished data records and manuscripts available at the Fisheries Research Board of Canada Biological Station, Nanaimo. These sources are listed in Table XVII together with average lengths in centimetres at

TABLE XVIII. Average length in centimetres at stated time periods as estimated from the growth curve of Fig. 7.

Date	t (days)	Ln l	l
April 20	0	1.250	3.49
May 20	30	1.809	6.10
June 19	60	2.133	8.44
July 19	90	2.359	10.58
August 18	120	2.562	12.96
September 17	150	2.754	15.70
October 17	180	2.923	18.59
November 16	210	3.070	21.54
December 16	240	3.197	24.45
January 15	270	3.310	27.37
February 14	300	3.404	30.07
March 16	330	3.480	32.45
April 15	360	3.557	35.04
May 15	390	3.728	41.58
June 14	420	3.838	46.41
July 14	450	3.909	49.83
August 13	480	3.950	51.91

average time-periods. Average lengths for central British Columbia pink salmon, as computed from the growth curve in Fig. 7, are presented in Table XVIII. These are plotted as a solid line in Fig. 9 while length data from various sources are plotted as individual sample measurements.

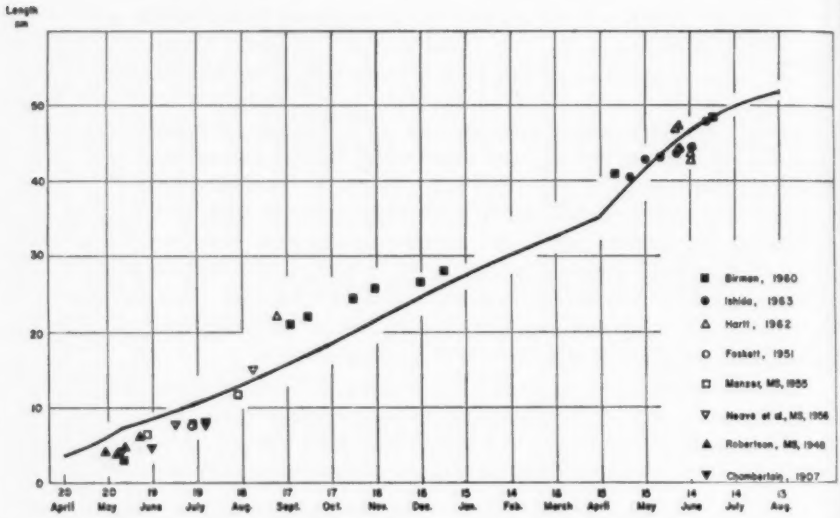


FIG. 9. Growth curve for central British Columbia pink salmon compared with data from other investigations, from Table XVII.

Several differences between the growth curve developed here and the observations cited in Table XVII are apparent. During the younger stages the observations listed in Table XVII lie below the curve. These might indicate either later arrival into the sea of the different stocks, incomplete sampling of populations non-randomly dispersed, or the use of size-selective methods. The abrupt change in size when sampling is shifted from coastal to offshore waters in early September is apparent. Hartt's (1962) data (incompletely reproduced in Table XVII) demonstrates the variation between average sizes of samples obtained from different areas along the Aleutian Islands. In general the larger sizes are associated with the easternmost samples. It is to be expected that the various stocks of Pacific pink salmon exhibit not only unique timing characteristics of life history events, but also differences in growth responses to similar or dissimilar environmental opportunities. It is not possible, however, to decide from these data which of the above causes have produced the evident anomalies of growth. However, it is remarkable that the differences between the various data are not greater. As a species, pink salmon develop from fry to adult under widely varying conditions along the eastern and western shores of the North Pacific, yet as maturing adults they are quite similar in size.

ACKNOWLEDGMENTS

Data presented and analysed in this report were assembled by a large number of personnel of the Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C., who can only be collectively acknowledged. Samples obtained on the high seas resulted from the efforts of the Station's Marine Salmon Investigation, headed by Dr Ferris Neave. Shore samples of the 1962 catch were produced by the Station's Salmon Stock Assessment Investigation, headed by Dr M. P. Shepard. Drs Neave and Shepard have kindly criticised the manuscript and materially contributed to its final form. Dr T. Ishida of the Hokkaido Regional Fisheries Research Laboratory, Japan, was indeed kind to supply us with original measurements of Asian pink salmon. The manuscript was further constructively criticised by Drs P. A. Larkin and W. E. Ricker of the Biological Station at Nanaimo. To these people, named and unnamed, the authors are grateful.

REFERENCES

BIRMAN, I. B. 1960. On the period of formation of the annual rings on the scales of Pacific salmon and the rate of growth of Pinks. *Doklady Akademii Nauk SSSR*, **132**(5): 1187–1190. [FRB Translation Series, No. 327.].

CHAMBERLAIN, F. M. 1907. Some observations of salmon and trout in Alaska. *Rept. U.S. Bur. Fish.*, Doc. No. 627, pp. 5–112.

FOSKETT, D. R. 1951. Young salmon in the Nanaimo area. *Fish. Res. Bd. Canada, Prog. Rept. Pacific Coast Sta.*, No. 86, p. 18.

HARTT, A. C. 1962. Observations on pink salmon in the Aleutian Island area, 1956–1960. H. R. MacMillan Lectures in Fisheries, Symposium on Pink Salmon 1960, University of British Columbia, Institute of Fisheries, pp. 123–133.

INPFC. Annual reports of the International North Pacific Fisheries Commission for the years 1956, 1962, and 1963. Vancouver, Canada.

ISHIDA, T. 1963. Consideration on the differences in body length, sex ratio and body weight in the pink salmon catches of long-line and gill-net of the Japanese land-base fisheries, with special reference to mesh selectivity. *Bull. Hokkaido Reg. Fish. Res. Lab.*, No. 26, pp. 67–72.

LEBRASSEUR, R. J., AND W. BARNER. MS, 1964. Midwater trawl catches of juvenile pink and chum salmon. Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.

MANZER, J. I. MS, 1955. Size and sex of juvenile salmon. Annual Report of the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C., pp. 4–5.

MANZER, J. I., AND M. P. SHEPARD. 1962. Marine survival, distribution and migration of pink salmon off the British Columbia coast. H. R. MacMillan Lectures in Fisheries, Symposium on Pink Salmon 1960, University of British Columbia, Institute of Fisheries, pp. 113–122.

NEAVE, F., J. I. MANZER AND G. T. TAYLOR. MS, 1956. Distribution and tagging of juvenile salmon. Annual Report of the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C., p. 9.

PARKER, R. R. 1962. Tag failure associated with a net fishery as a source of experimental error. *J. Fish. Res. Bd. Canada*, **19**(2): 315–320.

1963a. On the problem of maximum yield from North Pacific sockeye salmon stocks. *Ibid.*, **20**(6): 1371–1396.

1963. Effects of formalin on length and weight of fishes. *Ibid.*, **20**(6): 1441–1455.

1964. Estimation of sea mortality rates for the 1960 brood-year pink salmon of Hook Nose Creek, British Columbia. *Ibid.*, **21**(5): 1019–1034.

ROBERTSON, G. MS, 1948. Some interesting observations on the chum and pink salmon fry in Departure Bay, 1948. Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.

Distribution and Synonymy in the Pacific Ocean, and Variation, of the Greenland Halibut, *Reinhardtius hippoglossoides* (Walbaum)[1,2]

By Carl L. Hubbs[3] and Norman J. Wilimovsky[4]

ABSTRACT

Long known in the Pacific Ocean from a single specimen from east-central Japan, the very distinctive flatfish genus *Reinhardtius* has been shown since 1930 to maintain a population of commercial significance from northern Japan to northwestern Bering Sea. It is now found to be common also in eastern Bering Sea, and to occur also just south of the tip of the Alaska Peninsula, in northern and central California, and even at the extreme north of Baja California, Mexico. Japan and the Californias appear to be inhabited by non-breeding expatriates, whose wanderings are attributable to the free-swimming habits and prolonged early pelagic development of the species. Lack of records between the Alaska Peninsula and California may possibly indicate actual absence, attributable to current pattern. Analysis of the only morphometric characters thought to be indicative of subspecific differentiation between the Pacific and Atlantic stocks discloses no basis for such separation, nor do any meristic characters disclose such a basis. The single species *Reinhardtius hippoglossoides* is therefore regarded as a uniquely undifferentiated amphiboreal taxon. The chief distinction between the ocean stocks lies in the number of vertebrae, but the differentiation (probably genetic) is not beyond the racial level. The difference in vertebral numbers, surprisingly, is not paralleled by a difference in numbers of dorsal or anal rays; nor is there any marked correlation between vertebral and ray numbers. As expected, the numbers of dorsal and anal rays are found to be positively correlated, and the number of precaudal and caudal vertebrae to be negatively correlated. In this flatfish of relatively limited asymmetry the numbers of rays are virtually identical in the two pectoral fins. Two reversed examples of the species are reported.

INTRODUCTION

Recent recognition of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in commercial catches of other fish in eastern Bering Sea, and as stragglers in the eastern Pacific Ocean as far south as extreme northern Mexico, has prompted evaluation of the systematic status and distribution of this species in the Pacific. The investigation has provided data on its morphometric and meristic variation in the Atlantic as well as in the Pacific Ocean.

Reinhardtius, though confused by some fishermen with the arrowtooth flounder, *Atheresthes*, is a distinctive elongate pleuronectine flatfish (Fig. 1), having a straight lateral line and a very large mouth equipped with strong non-depressible teeth, uniserially set in the lower jaw. *Atheresthes* has a similarly formed lateral line, but differs in having the teeth usually barbed at the tip and arranged biserially in each jaw, with some of them depressible. In addition,

[1]Received for publication May 25, 1964.
[2]Contribution from the Scripps Institution of Oceanography, University of California San Diego, and from the Institute of Fisheries, The University of British Columbia.
[3]Scripps Institution of Oceanography, La Jolla, California.
[4]Institute of Fisheries, The University of British Columbia, Vancouver, Canada.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

Atheresthes has many fewer vertebrae and much larger scales, and is distinctive in the character of the gill-rakers, which are long and thin, and in the character of the pharyngeal teeth, which are small and biserial. In *Reinhardtius*, the rakers are massive and short, some scalelike, and the very large pharyngeal teeth form a single row. Other and even more notably characteristic features of *Reinhardtius* are the parallel olfactory laminae, lacking a rachis (the olfactory laminae are arranged transversely to a central rachis in *Atheresthes*—a primitive pattern, unique among the Pleuronectidae), and the distinctive, extremely thin otolith (Fig. 2). Other features of *Reinhardtius* that distinguish it from related genera are indicated by Norman (1934), Vernidub and Panin (1937) and by Pertseva-Ostroumova (1961). The Greenland halibut ranges widely in the northern parts of the Atlantic as well as the Pacific Ocean; the arrowtooth flounder is known only from the North Pacific, which is the major center of the pleuronectine flatfishes.

The very dark coloration of *Reinhardtius*, almost black on the eyed side and usually variously darkened on the blind side, has given rise to the vernaculars "chernyi paltus" (= black paltus) or "karasu garei" (= black flounder), the names most generally used by Russian and Japanese workers in the Far East. The Atlantic representative goes under a variety of common names (Hoek, 1904), but "Greenland halibut" is the most widely accepted term.

DISCOVERIES REGARDING *REINHARDTIUS* IN THE PACIFIC OCEAN

The Greenland halibut was first recorded in the Pacific Ocean by Ishikawa and Matsuüra (1897), who identified a specimen from Sagami Bay, Japan (at approximately 35° N. Lat., 139° E. Long.) with Günther's name for this species, *Hippoglossus groenlandicus*. In 1901, Jordan and Snyder established *Reinhardtius matsuurae* on the basis of the same stuffed example.

No new finds were reported from Japan until 1936, when Tanaka listed it for Kuji on the east coast of Honshû. It was not until 1931–32 that Soviet exploratory fishing located the species in Okhotsk Sea and in the northwestern part of Bering Sea, between Cape Navarin in Siberia and the Alaskan island of St. Matthew in the north-central part of Bering Sea. The northernmost record was based on five young specimens from the Gulf of Anadir (Musienko, 1954).

The occurrence of the species in eastern Bering Sea was noted by the junior author in 1960 while examining the catches of that year made by the exploratory fishing vessel *John R. Manning* of the United States Bureau of Commercial Fisheries. In 1961 one specimen was taken by the International North Pacific Halibut Commission just south of the tip of the Alaska Peninsula. These records are detailed, with others, in the Appendix.

The abundance of the species in the eastern part of Bering Sea, and its prolific reproduction there, was dramatically indicated by the taking of about 500 young specimens from the stomach of one northern fur seal (*Callorhinus ursinus*), which was caught 93 km north-northeast of St. Paul Island on August 24, 1963.

FIG. 1. *Reinhardtius hippoglossoides:* an adult (SIO 62-249-64A) 639 mm in standard length taken in Baja California, 8 km south of United States–Mexico border on May 9, 1962. Photographs by Scripps Institution of Oceanography.

FIG. 2. Otoliths (sagittae) from an adult specimen (CAS 27029) 379 mm in standard length, obtained at Fort Bragg, California. Left otolith above, right below; both faces shown (concave to left, convex to right). The left sagitta measures 6.0 × 8.5 mm; the right, 6.1 × 7.7 mm. The cross line in the upper right figure represents a repaired accidental break of its thin, fragile structure. Photographs by Mr W. I. Follett, California Academy of Sciences.

No specimens have as yet come to light from the Gulf of Alaska, southeastern Alaska, British Columbia, Washington, or Oregon. The senior author was, therefore, greatly surprised to receive an adult specimen (Fig. 1) taken on May 9, 1962, 8 km south of the Mexican border, at a depth of 14.5–16.5 m. It is perhaps significant that this specimen was caught in a cold period, as was the specimen reported by Abe (1963) from Sagami Bay, Japan. The discovery of this specimen led California fishery workers and ichthyologists to examine the catches of the superficially similar arrowtooth flounder (*Atheresthes stomias*) in the mink-food fishery of central and northern California, with the result that six adult specimens of *Reinhardtius* have been secured (listed in the Appendix). The first of these was recorded by Best (1963). All were taken in 1962 and into early July 1963.

A second Pacific species, *Reinhardtius oleosus*, was assigned to this genus by Tanaka (1918), who later (Tanaka, 1931) uncritically suggested that *Atheresthes evermanni*, and possibly his *R. oleosus*, were synonyms of *R. matsuurae*. Examination of the original description of *R. oleosus* (available to us in translation) makes fully clear its identity with *Atheresthes evermanni*.

Other recent literature on the species has been concerned with the life history, growth, bathymetric distribution, and fishery of the species in the northwestern Pacific and Bering Sea (cf. particularly Musienko, 1954; and Mikawa, 1963).

As can be noted from the following synonymy several workers have questioned the specific distinctness of the Pacific representative from the Atlantic form, but the first published comparison was that of Vernidub and Panin (1937). These authors indicated significant differences between specimens from the Atlantic and Pacific oceans only in proportions involving the relative depth and length of the caudal peduncle and the relative lengths of the upper jaw and head. On the basis of these findings, utilizing 36 specimens from Okhotsk and Bering seas but only 8 from the Atlantic, Vernidub and Panin chose to recognize the Pacific form as a subspecies, *Reinhardtius hippoglossoides matsuurae*. They did so despite the fact that no overlap was indicated in the two morphometric characters thought to be reliable. Most subsequent investigators have chosen to adopt this designation, but some have recognized the Pacific form variously as a full species or as a synonym of the Atlantic *R. hippoglossoides*. As we show below, our data indicate that the populations of the Atlantic and Pacific oceans are not separable even at the subspecies level, on the basis of any character examined by us.

SYNONYMY FOR THE PACIFIC OCEAN POPULATION

To assist in tracing its nomenclatural history and literature, the following synonymy has been prepared to cover the accounts we have found of the occurrence, characters, life history, and fishery of the Greenland halibut in the Pacific Ocean. Citations listed only in this synonymy are not included in the References. Russian names printed in Cyrillic characters are transliterated.

Reinhardtius hippoglossoides (Walbaum)

Hippoglossus groenlandicus.—Ishikawa, C., and K. Matsuūra. 1897, Preliminary catalogue of fishes, including Dipnoi, Cyclostomi and Cephalochorda, in the collection of the Natural History Department, Imperial Museum of Tokyo: 25 (listed, Sagami Bay).

Reinhardtius matsuurae.—Jordan, D. S., and J. O. Snyder. 1901, J. Coll. Sci. Imperial Univ., Tokyo, 25: 309, pl. 16 (original description; Sagami Bay)—Jordan, D. S., and E. C. Starks. 1906, Proc. U. S. Nat. Mus., 31: 196 (description, after Jordan and Snyder)—Jordan, D. S., S. Tanaka, and J. O. Snyder. 1913, J. Coll. Sci. Imperial Univ., Tokyo, 33: 322 (listed; Misaki, Sagami)—Soldatov, V. K., and G. U. Lindberg. 1930, Bull. Pac. Fish. Inst. [in Russian], 5: 398 (after Jordan and Snyder; hypothetical in Far East of USSR)—Tanaka, S. 1931, J. Fac. Sci. Imperial Univ., Tokyo, 3: 47 (listed; *R. oleosus* and *Atheresthes evermanni* wrongly considered as synonyms; northern Japan)—Norman, J. R. 1934, A systematic monograph of the flatfishes (Heterosomata), British Museum: 290 (listed; identity with *R. hippoglossoides* suggested)—Jensen, A. S. 1935, Mem. Acad. Roy. Sci. et Let. Dan., Sec. Sci., (9) 6, 4: 1, footnote (listed; after Norman)—Tanaka, S. 1936, The fishes of Japan, Tokyo [in Japanese]: 259 (comparison; Kuji, Honshû, and Hokkaido)—Okada, Y. 1938, A catalogue of vertebrates of Japan, Maruzen Co., Tokyo: 264 (listed; Misaki)—Okada, Y., and K. Matsubara. 1938, Keys to the fishes and fish-like animals of Japan, Sanseido Co., Japan [in Japanese]: 428 (key; Sagami).

Reinhardtius hippoglossoides matsuurae.—Andriyashev, A. P. 1935, Issled. Morey SSSR [in Russian], 22: 138 (distribution; Okhotsk and Bering seas)—Andriyashev, A. P. 1937, Issled. Morey SSSR [in Russian], 25: 321 (biology; distribution; Okhotsk and Bering seas) [translation published as Special Scientific Report: Fisheries, 145, U. S. Fish and Wildlife Service, 1955]—Taranets, A. J. 1937, Bull. Pac. Sci. Inst. Fish. and Ocean. [in Russian], 11: 143 (distribution; western Bering Sea and Japan)—Vernidub, M. F., and K. I. Panin. 1937, Uchen. Zap. Leningrad [in Russian], 15: 250 (description; comparisons; biology; distribution)—Andriyashev, A. P. 1939, Ocherk zoogeografii i proiskhozhdeniia fauny ryb Beringova moria i sopredelbnykh vod. Leningrad [in Russian]: 71, (distribution)—Shmidt, P. Y. 1948, Ryby Tikhogo Okeana. Moskva: 94 (distribution; depth range; Bering Sea)—Esipov, V. K. 1949, *in* L. S. Berg [editor], Promyslovye Ryby SSSR, VNIRO [in Russian]: 695 (listed; North Pacific)—Shmidt, P. Y. 1950, Ryby Okhotskogo Morya [in Russian]: 225 (comparisons; after Vernidub and Panin; biology; distribution; North Pacific)—Moiseev, P. A. 1953, Izv. TINRO [in Russian], 40: 140 (distribution; biology; fishery) [Fish. Res. Bd. Canada, Translation Series No. 119.]—Musienko, J. N. 1954, Trudy Inst. Okean. [in Russian], 11: 68, figs. 1, 5 (distribution; counts and measurements; young from Anadir, Siberia)—Polutov, I. A., and V. N. Tripolskaya. 1954, Izv. Tikh. Okean., 41 (listed; Aniva and northern Hokkaido; quoted from Pertseva-Ostroumova, 1961)—Rass, T. S. [editor]. 1955, Trudy Inst. Okean. [in Russian], 14: 56–58, 1 fig. (distribution; biology; fishery)—Nikolski, G. W. 1957, Spezielle Fischkunde. Berlin: 487 (western Pacific, Bering Sea to Japan; compilation)—Musienko, J. N. 1957, Trudy Inst. Okean., 20: 312 (age and growth; distribution in Far Eastern Seas) [Translation published by American Institute of Biological Sciences, 1959]—Novykov, N. P. 1960, Rybnoe Khoziaistvo [in Russian], 36: 12–15 (distribution; biology; fishery) [Fish. Res. Bd. Canada, Translation Series No. 329.]—Musienko, J. N. 1961, Trudy Inst. Okean. [in Russian], 43: 282 (listed; young; Karaginski Bay)—Khrapkova, N. V. 1961, Trudy Inst. Okean. [in Russian], 43: 291, 303 (habitat; relation between density and food; Kamchatka Bay)—Pertseva-Ostroumova, T. A. 1961, Trudy Inst. Okean. [in Russian], 43: 347 (listed; Far Eastern Seas)—Pertseva-Ostroumova, T. A. 1961, Razmnozhenie i razvitie kambal. Akad. Nauk: 33, 202, 394, 426 (development; spawning; larva; seasonal occurrences; descriptions and comparisons)—Mikawa, M. 1963, Bull. Tohoku Reg. Fish. Res. Lab. [in Japanese], 23: 1 (description; detailed ecology; catches; distribution).

Reinchardtius [*sic*] *hippoglossoides matsuurae.*—Nikolsky, G. V. 1950, Chastnaya Ikhtiologiya, Gosudarstvennoe Izdatel'stvo "Sovetskaya Nauka," Moskva [in Russian]: 367 (western Pacific, Bering Sea to Japan; compilation)—Andriyashev, A. P. 1954, Ryby Severnykh Morey SSSR [in Russian]: 475 (characters; after Vernidub and Panin; Cape Navarin to St. Matthew Island, at 110 to 250 m)—Nikolsky, G. V. 1954, Chastnaya Ikhtiologiya, Gosudarstvennoe Izdatel'stvo "Sovetskaya Nauka," Moskva, 2nd edition [in Russian]: 382 (western Pacific, Bering Sea to Japan; compilation)—Nikolsky, G. V. 1961, Special Ichthyology, Translation, OTS 60–21817: 441 (comparisons; life history; range; western Pacific, Barents Sea [*sic* = Bering Sea] to Japan; compilation).

Reinhardtius hippoglossoides matsuurai.—Tomiyama, I., and T. Abe. 1958, Fishes *in* Encyclopaedia Zoologica, II [in Japanese]: 43, Fig. 122 (life history; comparison; distribution; Sagami Bay, northwestern Bering Sea, and Central Okhotsk Sea)—Abe, T. 1963, Bull. Tokai Regional Fish. Res. Lab., 37: 30 (synonymy for Pacific Ocean; off Cape of Manazuru, Sagami Bay, Japan, in cold-water season; relation to Atlantic form).

Reinhardtius matsuurai.—Matsubara, K. 1955, Fish morphology and hierarchy, II [in Japanese]: 1267 (key; Sagami)—Kasahara, H. 1961, Fisheries Resources of the North Pacific Ocean. The University of British Columbia: 81 (distribution; fishery).

Reinhardtius hippoglossoides.—Taranets, A. Y. 1933, Vest. Dal. Fil. Akad. Nauk SSSR [in Russian], 1–3: 74 (listed; Okhotsk and Bering seas)—Schmidt, P. J. 1934, Proc. Fifth Pac. Sci. Cong., 2: 614 (west coast of Kamchatka, Bering Sea; as food fish; listed p. 616 as *Reinhardtius platessoides*, an obvious *lapsus*)—Schmidt, P. J. 1934, Proc. Fifth Pac. Sci. Cong., 5: 3797 (range; north Pacific Ocean; as subspecies or race of typical form)—Andriyashev, A. P. 1944, Priroda [in Russian], 1: 46 (as example of amphiboreal distribution)—Andriyashev, A. P. 1954, Ryby Severnykh Morey SSSR [in Russian]: 474, fig. 278 (description; synonymy; growth; range)—Hayashi, K. 1958, Monthly Rept. Hokkaido Reg. Fish. Lab. [in Japanese], 15 (3) (counts and measurements; Pacific; quoted from Mikawa, 1963)—Hotta, H. 1961, Comparative study of the axial skeleton of Japanese Teleostei [in Japanese]; 118, fig. 185 (description of skull and vertebrae)—Best, E. A. 1963, Calif. Fish and Game, 49: 213 (first California record, from Gulf of Farallones).

RANGE OF *REINHARDTIUS* IN THE PACIFIC

The discoveries outlined earlier enable us to define the known range (Fig. 3) of *Reinhardtius hippoglossoides* in the Pacific as primarily encompassing the seas from off the eastern shores of Honshû north of Kinkazan, Hokkaido, southern and eastern Sakhalin, the Kurile Islands, and western and eastern Kamchatka, to the northern and eastern parts of Bering Sea. Records from the east coast of central Honshû, Japan and from northern and central California and the extreme north of Baja California, Mexico, are apparently attributable, as is noted below, to stragglers. The status of the species between the Alaska Peninsula and the northern border of California remains to be determined.

The remarkable increase during recent years in the known range of the Greenland halibut in the North Pacific leads one to wonder whether this fish has been expanding its range, or whether it was previously overlooked there, either because the appropriate fisheries had not expanded into depths or areas where the species is now found, or because it had been confounded with the arrowtooth flounder, *Atheresthes*. We suspect that changes in the fishery are the major factor, along with the recent expansion in fisheries research and ichthyological activity. On the Asiatic side, the commercial importance, even the known occurrence of the species throughout its major range, was not discovered until the Russians undertook exploratory trawling in 1931–32 and subsequent years. The single adult specimen from northernmost Baja California was taken as a result of coincidence, for it was an emaciated fish that had strayed into shallow water. The taking of six adults in California is attributable to the expansion of the trawl fishery into appropriate deep waters and to the direction of attention to the species as a result of its discovery south of the United States–Mexican border. The lack of earlier records from northern waters, despite the extensive line fisheries for Pacific halibut and Pacific cod, is understandable, because at that time such extraneous fishes were not retained by the essentially single-species fisheries.

Sporadic Southward Occurrence

The occurrence of *Reinhardtius* over such a wide latitudinal range on each side of the Pacific seems to be attributable at least in part to sporadic dispersals to the southward.

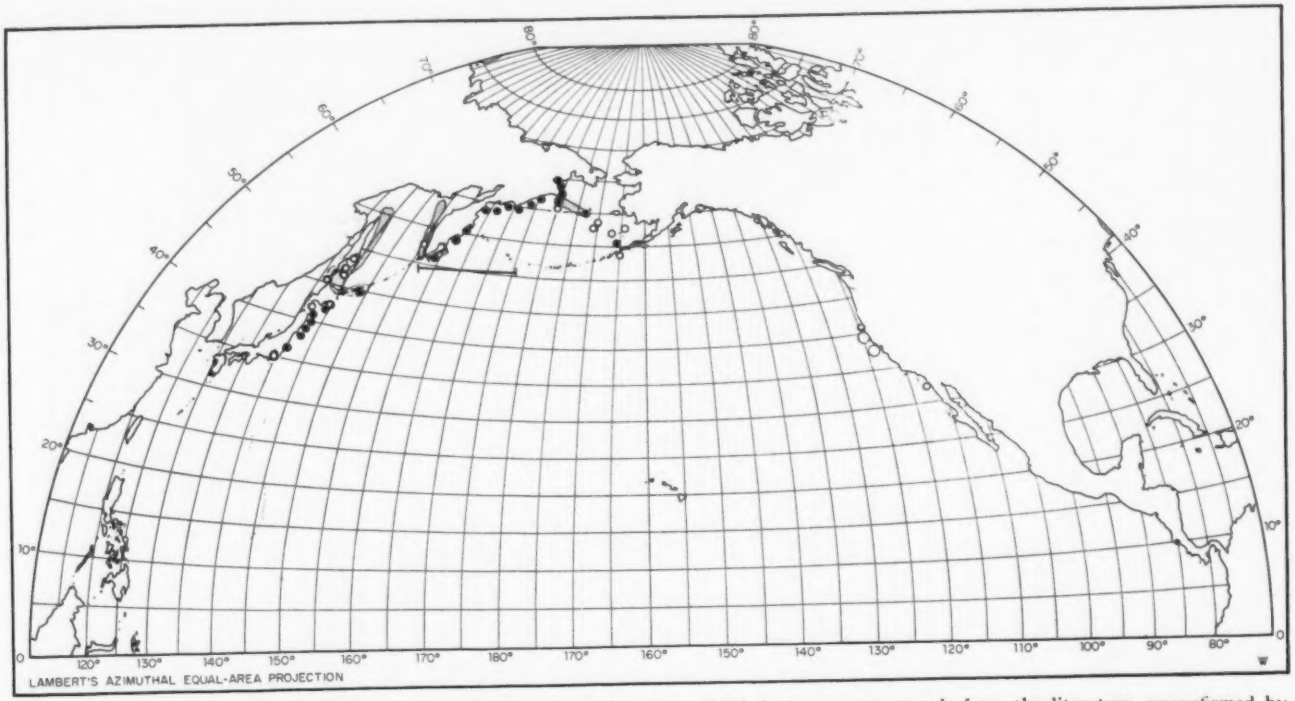


FIG. 3. Distribution in the Pacific Ocean of *Reinhardtius hippoglossoides*. Solid dots represent records from the literature, unconfirmed by re-examination of specimens; small hollow circles represent reported specimens re-examined by us and previously unreported specimens; the two large circles off California represent locations of capture known only approximately; the solid lines represent the courses of Japanese fishery exploring vessels along which Greenland halibut were trawled; stippled areas represent the Soviet fishing grounds (from Rass, 1955).

The early record from Sagami Bay, Japan, for decades the only record of the species from the Pacific, was not duplicated until April 8, 1963, when one adult was taken during a season of unusually cool water (12.7° C near the bottom) and when other cold-water fishes were also taken at this usually warm-temperate region (Abe, 1963). The known occurrence of this species so far south on only two occasions may be interpreted as very unusual and sporadic, because ichthyologists have been very active in this area, near Misaki, which has long been famed for varied, deep-water fishing. The recent capture of a specimen of this and of other boreal fishes so far south in Japan during a period of cold water seems to have been paralleled by the recent discovery (Boyar, 1964) of this species in the Gulf of Maine, in unusually shallow water, during a time (February 1963) when "the water temperatures in the area of capture were 1.5 to 2.5° C colder than in the past 3 years." The Gulf of Maine occurrences were indicated as being at record shallow depths of 35–55 fathoms (65–101 m), but Rass (1955) gave the depth range for the species in Asian waters as 70–700 m and Musienko (1954) reported young from the Gulf of Anadir at depths as shallow as 18–40 m. We have material from commercial catches made in depths as shallow as 52 and 56 m, and the one specimen, an adult, known from Baja California came from a depth of only 14.5–16.5 m. The specimen taken in Sagami Bay in 1963 came from a depth of only 20 m (Abe, 1963). A young specimen from the Canadian Arctic (see Appendix) was taken at the depth of only 14–18 m. It is, however, the consensus of workers on the Greenland halibut that in its northern home waters this species, especially as breeding adults, inhabits deep water, generally beyond the continental shelf.

In the Atlantic the distribution is apparently similar. Dunbar and Hildebrand (1952: 110–111), in reporting the first material from the Canadian Arctic in Ungava Bay, from which no other species of flatfish had been taken, stated: "General distribution subarctic and arctic, known from northwest Greenland and Spitzbergen south to Norway and Newfoundland, rarer as far as Cape Cod." Records from Georges Bank, off New England, and from southwest of Ireland are listed in the Appendix.

It seems obvious that the species is not well established, if it reproduces at all, anywhere in the far-southern part of its range. All California records are of adults. Very young have been taken in abundance in the far north, but never toward the south: witness the finding, already mentioned, of about 500 young from the stomach of a single fur seal in Bering Sea, and the collection of 90 young from western Greenland (at 69°30′ N. Lat., 50°32′ W. Long.) made available to us by the Universitetets Zoologiske Museum, København.

The seemingly sporadic occurrence of the species to the southward may be attributed either to the free-swimming tendency of the adults, or to the prolonged drift of the protracted early stages, or to both of these factors. Jensen (1935) remarked on the observations that this flatfish (which significantly is much less asymmetric than most) does not consistently remain, as nearly all flatfishes do, on the bottom, "but at times comes up into the intermediate water-layers in pursuit of other fishes." He also stated, quoting Paul Hansen, that "apparently

large circles on California represent locations of capture known only approximately; the solid lines represent the courses of Japanese fishery exploring vessels along which Greenland halibut were trawled; stippled areas represent the Soviet fishing grounds (from Rass, 1955).

the Greenland halibut swim like ordinary fishes with the dorsal edge (fin) upwards." He further noted that the species undergoes a prolonged larval development, retaining bilateral symmetry to lengths of 54–57 mm, and stated that "the pelagic mode of life ends probably about a length of 70 mm., possibly even a little over that." Mikawa (1963) noted the occurrence of a higher proportion of smaller examples in more southern latitudes and indicated that the fish off Japan are immature.

The southward spread of the Greenland halibut is probably effected largely by the three main northern cold currents, the Oyashio Current in the western Pacific, the California Current, and the Labrador Current. The lack of records between the Alaska Peninsula and northern California, despite the trend in recent years toward deep-water trawling and extensive experimental fishing at varied depths in those areas, may find an explanation in the pattern of the currents. Young fish or perhaps even adults stemming from the population in the northwestern Pacific and from the population that likely exists off the south side of the Aleutian chain are presumably carried eastward by the North Pacific Drift. Those that happen to be on the north side of the current are apt to be caught in the Alaskan Gyre, whereas those that are on the south side of the Drift presumably are carried far southward, where occasional individuals may find bottom along the coast of northern and central California.

Recent oceanographic studies in the subarctic Pacific region (Dodimead, 1961; Dodimead *et al.* 1963) disclose a number of parameters in the physical environment that seem to have roughly the same area as that occupied in abundance by *Reinhardtius*. The notable correlated parameters are colder temperatures at the surface, at 10 m, and at "top of the halocline" or "bottom of upper zone". The area of known *Reinhardtius* abundance fits well the locations of the western gyres — those of Okhotsk Sea, Western Subarctic, and Bering Sea, constituting the Western Subarctic Upper Zone Domain — as opposed to the location of the Alaskan Gyre and the California current system to the southward, comprising the Alaskan Stream, Central Subarctic, and Transitional upper zone domains. Essentially similar is the correlation with geographically corresponding lower zone domains.

The occurrence of *Reinhardtius hippoglossoides* in the northeastern as well as the northwestern Pacific finds a partial parallel in the occurrence off western America of the large Asiatic flounder, *Clidoderma asperrimum* (Temminck and Schlegel). Welander *et al.* (1957) reported 2 specimens that had been caught off Vancouver Island on March 9, 1955. We understand that a few others have since been landed from that area.

REVERSED EXAMPLES

No reversed (left-eyed) specimens of *Reinhardtius* have been reported from the Pacific Ocean, and only one (Norman, 1934: 290), so far as we are aware, from the Atlantic Ocean. Dr Jørgen Nielsen, however, informs us that Universitetets Zoologiske Museum, København has two reversed specimens from Greenland: one, from Lichtenau Fjord, taken in 1914, and one from Sydprøven, at

60°27′ N. Lat., 45°34′ W. Long., taken in 1921. Obviously, *Reinhardtius* is one of the many flatfishes that are only occasionally reversed (Hubbs and Hubbs, 1945: 230–250).

VARIATION OF *REINHARDTIUS*, AND SYSTEMATIC STATUS OF THE PACIFIC POPULATION

The varied opinions that have been expressed regarding the systematic status of the population of *Reinhardtius* in the Pacific Ocean are indicated above in the synonymy and in the adjacent text. Inasmuch as the Soviet investigators indicated the Pacific and Atlantic material to differ to the degree of nomenclatural significance in only two morphometric relations, namely between upper-jaw length and head length, and between length and depth of caudal peduncle, major attention has been paid by us to an analysis of those dimensions. Meristic characters have also been analyzed, though previously no strong differences in these respects have been indicated.

The material utilized in these analyses is listed in the Appendix.

Morphometric Characters

Over a wide size range of specimens we have measured the four body parts, just mentioned, according to the following criteria:

Head length: measured in millimeters (or to 0.1 mm in small specimens) from the anteriormost edge of the upper lip to the farthest point on the opercular membrane (measured from point to point, not as a projection), so as to give the maximum obtainable dimension after any distortions on preservation have been rectified as far as possible by manipulation of the specimen.

Upper-jaw length: similarly measured, from point to point, so as to give the maximum dimension from front of upper lip to most posterior point at either the upper-posterior or lower-posterior end of the maxillary.

Length of caudal peduncle: distance in an oblique line from extreme, fleshy end of anal base to caudal base on midline. The latter point is determined by the line of flexure obtained when the caudal fin is moved back and forth while the point of the dividers or calipers is pressed down gently.

Depth of caudal peduncle: the minimum vertical depth, measured with care to avoid unnatural depressions.

Instead of expressing the results in ratios of upper-jaw length to head length and of caudal-peduncle depth to peduncle length, as Vernidub and Panin (1937) did, we have simply plotted (Fig. 4–5) each of the four sets of dimensions against the standard length (from anteriormost point of upper lip to caudal base, measured after distortions due to preservation have been rectified). The measurements for the Atlantic specimens are graphed as crosses, those for the Pacific specimens as hollow dots. On the first draft the material from several parts of the Pacific were graphed by distinctive symbols, but these distinctions were abandoned on the final copy, for purpose of clarity and because no significant regional differences were indicated.

An examination of the graphs (Fig. 4–5) completely fails to verify the indication by Vernidub and Panin (1937) that non-overlapping proportional relations distinguish the Pacific material of *Reinhardtius* from the Atlantic stock. Since essential agreement is shown for all four body dimensions, no significant difference can be expected in the ratios that these authors used to express their data. It is significant that they utilized only 36 specimens from

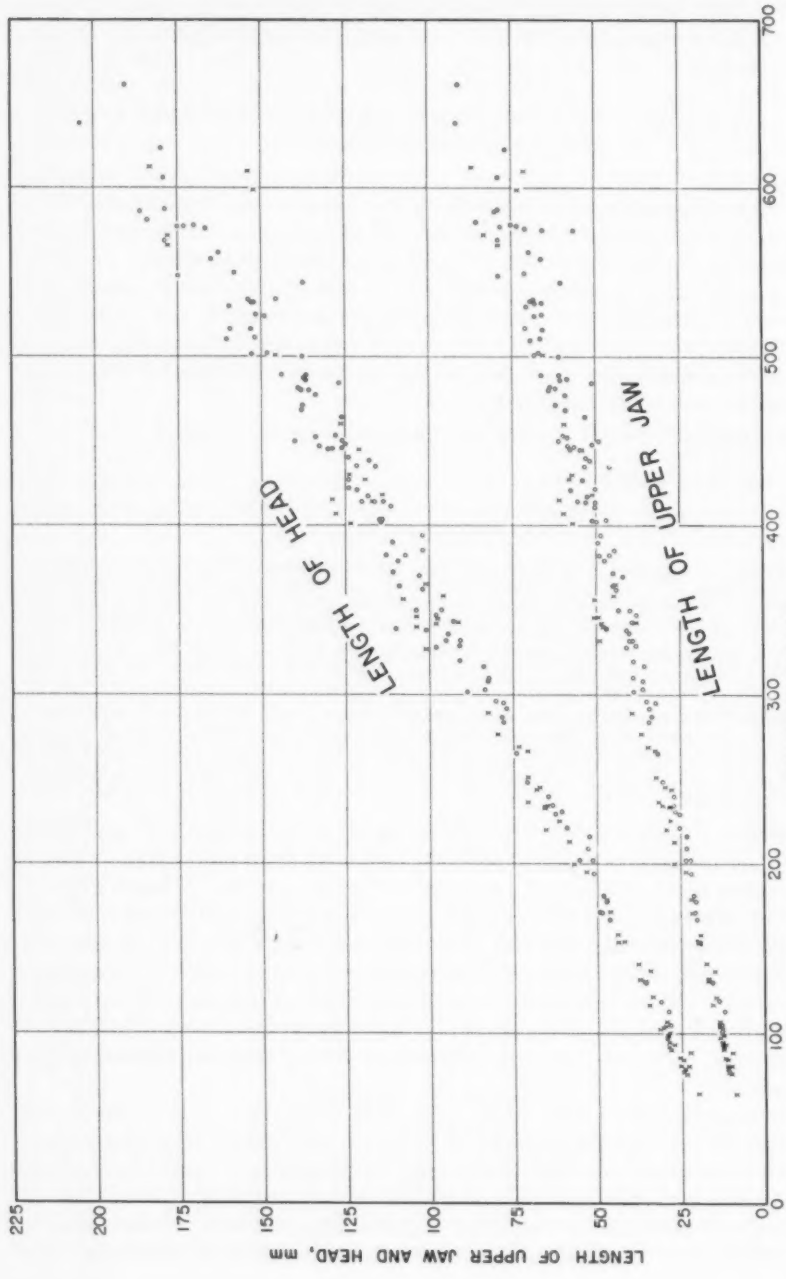


FIG. 4. Length of head and length of upper jaw in *Reinhardtius hippoglossoides* from various localities in the Pacific Ocean (hollow dots) and the Atlantic (crosses), plotted against standard length. Original graphing disclosed no significant differences between localities within either ocean.

FIG. 4. Length of head and length of upper jaw in *Reinhardtius hippoglossoides* from various localities in the Pacific Ocean (hollow dots) and the Atlantic (crosses), plotted against standard length. Original graphing disclosed no significant differences between localities within either ocean.

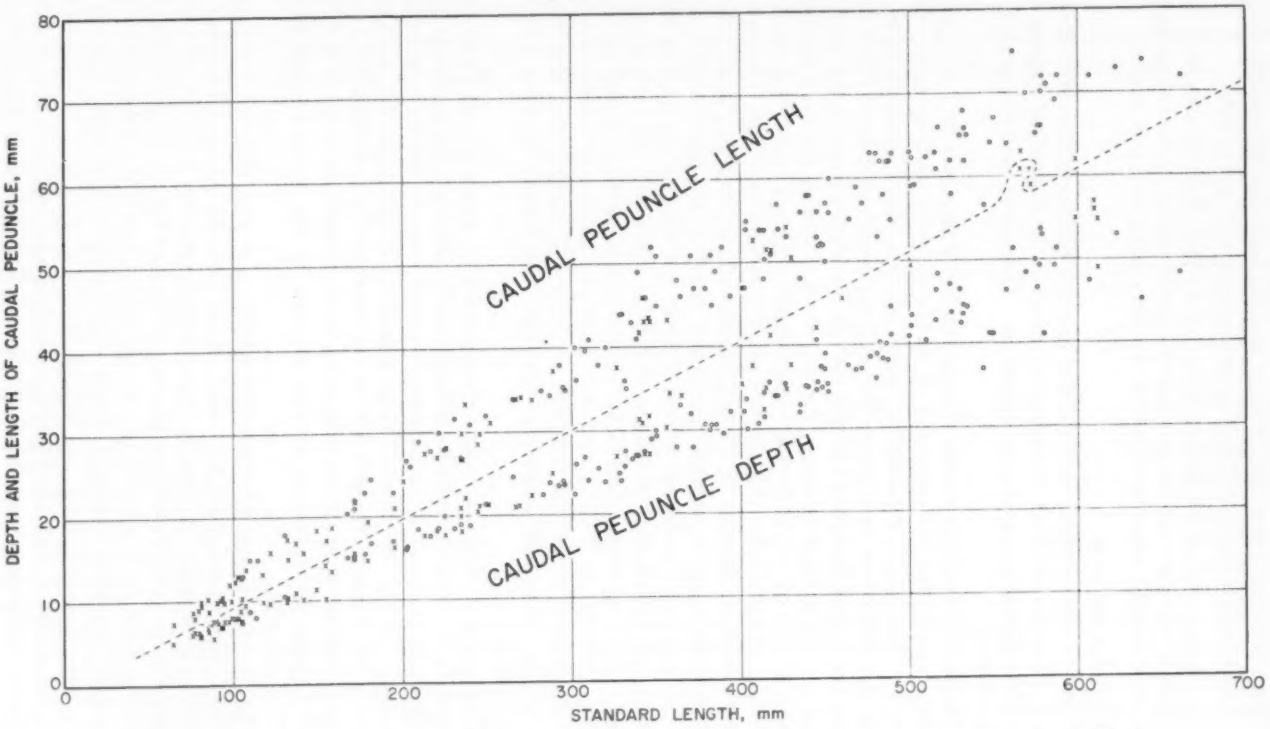


FIG. 5. Length and depth of caudal peduncle in *Reinhardtius hippoglossoides* from the two oceans, plotted as in Fig. 4.

the Pacific and only 8 from the Atlantic, and did not present their data in such a way as to take into account changing proportions with size of fish.

An examination of the graphs indicates a slight positive allometry for the head length and upper-jaw length, approximate isometry for the caudal-peduncle depth, and a slight negative allometry for the caudal-peduncle length.

Meristic Characters

Fin rays and vertebrae were counted in many specimens from several regions of each ocean in an effort to determine whether the Greenland halibut might have differentiated into species or subspecies. Gill-rakers were also counted on a few specimens.

Dorsal and anal ray counts include the last 2 elements as 1 ray, whether closely approximated, or separated as widely as the preceding rays. Caudal counts are "standard", representing branched rays plus 2; commonly, in large young and half-grown specimens, the ray that would later have bifurcated to become the lowest branched ray had not yet divided. Even in the adults the caudal rays are difficult to count, due to crowding and to the thick epithelium. All pectoral and all pelvic rays are enumerated, with the lowest one counted as single, and included even though very small; but what might be interpreted as a minute splint at the base of the uppermost main pectoral ray is not counted. The hypural complex is included as the last vertebra; the penultimate vertebra often bears 2 neural or haemal spines, or both, and may show a median vertical suture in various degree of development (but in this study this vertebra is consistently listed as one). Gill-raker counts proved confusing and somewhat arbitrary, because in *Reinhardtius* the rakers are short and toward the front of the lower arch grade into scale-like structures of varying size, and because other similar scaly rudiments are variously interpolated between the more obvious rakers.

The counts of dorsal and anal rays presented by Vernidub and Panin (1937) averaged higher in the Atlantic than in the Pacific, but our more numerous counts (Tables I and II) show no consistent differences between the material from the two oceans. In the Pacific, the counts, especially for the dorsal fin, average low along the east coast of Honshû and in the southern part of Sakhalin, but the difference falls far short of the subspecies level. Especially notable is the tremendous range, encompassing 26 rays (83–108) in the dorsal fin and 18 rays (62–79) in the anal.

The pectoral-ray counts (Table III) exhibit no striking differences regionally. The total observed range is 11–15, with either 13 or 14 the modal number and with the counts rather commonly about equally divided between 13 and 14. The pectoral-ray counts certainly provide no ground for taxonomic distinction.

The pectoral-ray counts in the Pacific (but not for the Atlantic) average very slightly higher on the right (eyed) than on the left (blind) side, but the difference is very small and is not wholly consistent, as is true of many pleuronectids, in contrast with most bothids (Hubbs and Hubbs, 1945: 254–263). The slightly higher average number of rays on the right side is reflected in the

TABLE I. Variation of *Reinhardtius hippoglossoides* in number of dorsal rays.

	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	No.	Mean
Pacific Ocean																												
Eastern Japan	..	..	..	2	..	1	5	4	2	5	2	1	..	1	1	..	..	..	1	..	..	..	..	..	..	..	25	91.24
S. part, Sakhalin Id.	1	..	..	..	..	..	..	2	1	2	1	2	1	..	1	..	..	..	..	..	..	..	..	..	..	..	11	91.91
Okhotsk Sea	..	..	..	..	..	1	..	2	3	2	3	2	4	3	5	2	2	..	1	1	..	..	1	..	..	..	32	95.22
Okhotsk Sea[a]	..	..	..	..	1	..	..	2	..	..	2	..	2	2	1	1	1	..	..	..	..	..	..	..	..	..	12	94.08
N. W. Pacific	..	..	..	..	1	..	..	..	1	1	3	3	3	3	5	4	..	..	..	..	..	..	..	..	..	..	24	95.04
Bering Sea[a]	..	..	..	..	1	..	1	1	4	2	2	1	1	..	3	2	1	1	..	1	..	..	..	..	..	..	21	94.14
Bering Sea[b]	..	..	..	..	..	..	..	1	3	1	1	1	4	..	1	1	4	3	1	..	..	..	..	..	..	..	21	95.90
Californias	..	..	..	..	..	..	..	1	..	2	..	1	..	..	1	..	..	1	..	..	..	..	..	..	..	..	6	94.17
Atlantic Ocean																												
(not specified)[a]	..	..	..	..	..	..	..	..	..	..	..	2	..	1	1	..	2	1	..	..	..	..	..	..	..	1	8	98.37
Grand Banks and Labrador	..	..	..	..	..	..	..	1	..	1	1	1	..	1	1	1	1	2	..	..	..	..	..	..	..	..	10	95.90
Greenland[a]	..	2	..	..	..	..	..	2	4	9	6	6	11	10	12	8	11	9	7	5	1	..	1	1	..	..	105	96.52
Totals																												
Pacific Ocean[d]	1	..	..	2	3	2	6	13	14	15	14	11	15	9	18	10	8	5	3	2	..	..	1	..	..	..	152	94.11
Atlantic Ocean	..	2	..	..	..	..	..	3	4	10	7	9	11	12	14	9	14	12	7	5	1	..	1	1	..	1	123	96.59
Grand Totals	1	2	..	2	3	2	6	16	18	25	21	20	26	21	32	19	22	17	10	7	1	..	2	1	..	1	275	95.22

[a]Counts from Vernidub and Panin (1937: 253), less one (on the assumption that they counted the last ray as single).

[b]Including 1 from just south of the tip of the Alaska Peninsula, with 97 rays.

[c]Including 3 from Iceland, with 96, 96, and 97 rays.

[d]Mikawa (1963) indicated the number of dorsal rays for the Pacific as "84–104": he probably counted the last ray as single, to yield a count 1 higher than ours.

TABLE II. Variation of *Reinhardtius hippoglossoides* in number of anal rays.

	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	No.	Mean
Pacific Ocean																				
Eastern Japan	..	..	..	..	..	4	4	5	4	4	..	2	1	..	1	..	..	..	25	69.80
S. part, Sakhalin Id.	..	..	1	..	1	2	..	2	..	2	1	1	1	..	..	..	..	..	11	69.36
Okhotsk Sea	..	..	..	..	..	2	2	6	2	1	7	6	..	1	2	2	..	1	32	71.78
Okhotsk Sea[a]	..	..	..	..	2	..	1	1	2	1	1	1	1	2	..	1	..	..	13	71.23
N. W. Pacific	..	..	..	..	..	..	1	2	2	2	6	6	4	1	1	..	..	..	25	72.20
Bering Sea[a]	..	2	1	..	1	..	1	3	2	5	2	3	3	..	..	..	..	..	23	70.04
Bering Sea[b]	..	..	..	..	..	..	2	2	1	2	3	2	2	4	1	2	..	..	21	72.67
Californias	..	..	..	..	..	1	1	1	..	1	2	..	..	..	..	1	..	..	7	70.86
Atlantic Ocean																				
(not specified)[a]	..	..	..	..	..	..	1	..	1	1	1	2	..	..	1	1	..	..	8	72.50
Grand Banks and Labrador	..	..	..	..	..	..	2	1	..	3	1	1	..	..	1	..	..	..	9	71.00
Greenland[c]	1	..	..	1	1	..	2	9	16	16	12	9	21	6	4	3	1	3	105	72.20
Totals																				
Pacific Ocean[d]	..	2	2	..	4	9	12	22	13	18	22	21	12	8	5	6	..	1	157	71.14
Atlantic Ocean	1	..	..	1	1	..	5	10	17	20	14	12	21	6	6	4	1	3	122	72.13
Grand totals	1	2	2	1	5	9	17	32	30	38	36	33	33	14	11	10	1	4	279	71.57

[a]Counts from Vernidub and Panin (1937: 253), less one (on the assumption that they counted the last ray as single).

[b]Including 1 from just south of the tip of the Alaska Peninsula, with 72 rays.

[c]Including 3 from Iceland, with 72, 74, and 74 rays.

[d]Mikawa (1963) indicated the number of anal rays in the Pacific as "63–77(81)"; he probably counted the last ray as single, to yield a count 1 higher than ours.

TABLE III. Variation of *Reinhardtius hippoglossoides* in number of pectoral rays.

	Number of pectoral rays						
	11	12	13	14	15	No.	Mean
Pacific Ocean							
Eastern Japan							
Left side	..	..	..	5	..	5	14.00
Right side	..	..	..	4	1	5	14.20
S. part, Sakhalin Id.							
Left side	..	1	4	5	1	11	13.55
Right side	..	2	5	3	1	11	13.27
Okhotsk Sea							
Left side	..	1	13	16	1	31	13.55
Right side	..	..	14	12	6	32	13.75
Northwest Pacific							
Left side	..	1	9	14	1	25	13.60
Right side	1	..	6	16	2	25	13.72
Bering Sea[a]							
Left side	..	..	8	11	2	21	13.71
Right side	..	..	7	13	1	21	13.71
Californias							
Left side	..	1	1	4	1	7	13.71
Right side	..	..	2	5	..	7	13.71
Atlantic Ocean							
Grand Banks							
Left side	..	..	3	5	..	8	13.63
Right side	..	..	3	7	..	10	13.70
Labrador							
Left side	..	..	1	1	..	2	13.5?
Right side	..	..	1	1	..	2	13.5?
Greenland							
Left side	..	1	39	36	6	82	13.57
Right side	..	2	53	44	4	103	13.49
Totals							
Pacific Ocean[b]							
Left side	..	4	35	55	6	100	13.63
Right side	1	2	34	53	11	101	13.70
Atlantic Ocean							
Left side	..	1	43	42	6	92	13.58
Right side	..	2	57	52	4	115	13.50
Grand Totals							
Left side	..	5	78	97	12	192	13.60
Right side	1	4	91	105	15	216	13.60

[a]Including one from just south of the tip of the Alaska Peninsula with 14–14 rays.

[b]Mikawa (1963), without distinguishing the sides, indicated the number of pectoral rays in the Pacific as "(10)12–15".

weak indication that the right fin may have more rays than the left fin when the count on the two sides is asymmetrical (Table IV), but the asymmetry is hardly significant (the 100P value for the Pacific is 22). There is no indication of asymmetry for the Atlantic material studied, and for the species as a whole the data indicate almost complete bilateral symmetry in pectoral-ray numbers—an unusual feature for a flatfish, but one that is consistent with the relatively limited asymmetry of *Reinhardtius* in general.

TABLE IV. Analysis of asymmetry in the pectoral-ray counts of *Reinhardtius hippoglossoides*. The statistical calculations follow those prescribed by Hubbs and Hubbs (1945).

	Counts		Counts Higher on:		100(L + R)	100 R	
	Symmetrical	Asymmetrical	L	R	N	L + R	100 P
Pacific Ocean	72	28	10	18	28	64	22
Atlantic Ocean	66	20	10	10	23	50	100
Total	138	48	20	28	26	58	35

The pelvic-ray counts (Table V) are of no taxonomic significance. The normal number is 6 on each side, but a few specimens, probably independently of locality, have 5 or 7 pelvic rays, and one specimen has 4 on one side. Out of a total of 139 specimens counted (109 from the Pacific, 30 from the Atlantic) the seven variant counts, left-side count given first, are as follows: 5–6(1), 6–4(1), 6–7(3), 7–6(1), 7–7(1).

Except in younger specimens the caudal rays, we find, almost invariably number 8 + 7 = 15 branched, or 9 + 8 = 17 total (branched plus 2). Among 109 specimens counted by us (99 from the Pacific and 10 from the Atlantic) 106 have the typical total count of 9 + 8 = 17; two have 8 + 8 = 16; one has 8 + 7 = 15. The agreement of *Reinhardtius* with the standard caudal-ray number of percomorph fishes may be significant, when the limited asymmetry and other rather generalized features of the genus are considered.

TABLE V. Variation of *Reinhardtius hippoglossoides* in number of pelvic rays.

	Number of pelvic rays					
	4	5	6	7	No.	Mean
Pacific Ocean						
Left side	..	1	103	2	106	6.01
Right side	..	..	100	4	104	6.04
Atlantic Ocean						
Left side	..	..	12	..	12	6.00
Right side	1	..	29	..	30	5.93

TABLE VI. Variation of *Reinhardtius hippoglossoides* in number of vertebrae.

	Precaudal					Caudal							Total vertebrae						
	17	18	19	No.	Mean	42	43	44	45	46	No.	Mean	60	61	62	63	64	No.	Mean
Pacific Ocean																			
S. Sakhalin Id.	..	8	3	11	18.27	..	..	..	9	2	11	45.18	..	..	..	6	5	11	63.45
Okhotsk Sea	8	21	1	30	17.77	..	3	5	15	7	30	44.87	..	3	6	19	2	30	62.67
N. W. Pacific	7	18	..	25	17.72	..	..	7	14	4	25	44.88	..	1	12	9	3	25	62.56
Bering Sea[a]	4	17	..	21	17.81	..	..	6	13	2	21	44.81	..	1	9	10	1	21	62.52
Californias	2	4	..	6	17.67	..	..	..	4	2	6	45.33	..	..	..	6	..	6	63.00
Atlantic Ocean																			
Greenland[b]	32	58	..	90	17.64	..	30	46	14	..	90	44.84	3	45	39	3	..	90	61.47
Labrador and Grand Banks	3	8	..	11	17.73	1	3	7	..	..	11	43.55	1	6	4	..	..	11	61.27
Totals																			
Pacific Ocean	21	68	4	93	17.82	..	3	18	55	17	93	44.92	..	5	27	50	11	93[c]	62.72
Atlantic Ocean	35	66	..	101	17.65	1	33	53	14	..	101	43.79	4	51	43	3	..	101	61.45

[a]Including 1 from just south of the tip of Alaska Peninsula, with 18+ 45 = 63 vertebrae.
[b]Including 2 from Ungava Bay, arctic Canada, each with 18 + 45 vertebrae.
[c]Mikawa (1963) indicated the number of vertebrae for the Pacific as "(60)61–64(65)".

Gill-rakers in *Reinhardtius*, as stated above, are so difficult to enumerate with confidence as to be of limited value. The counts recorded are as follows:

For the Pacific Ocean: on eyed side in 14 specimens, 3–6 + 12–16 = 15–20; on blind side in 14, 3–6 + 11–16 = 15–20.

For the Atlantic Ocean: on eyed side in 21 specimens, 3–5 + 11–15 = 14–19; on blind side in 14, 3–6 + 12–15 = 15–20. The mean for 27 total counts for the Pacific, ranging from 15 to 20, is 17.11; the mean for 35 counts from the Atlantic, ranging from 14 to 20, is 18.03. There is no suggestion that the gill-raker number can be used to separate local forms of this species.

After it appeared that the meristic data were virtually identical for the two oceans a difference was indicated by preliminary counts of vertebrae. An enlarged series of counts (Table VI), consequently taken, shows that a significant difference exists, and that the mean values seem to be relatively consistent in each ocean, but that the distinction falls far short of any accepted criterion for subspecies separation. The highly reliable t values are 2.5 for precaudal counts, 11.3 for caudal counts, and 12.9 for total counts. The average difference between the stocks of the two oceans is probably a true, genetic racial distinction, for it seems to be nearly constant within each ocean.

Inasmuch as it is usual for the numbers of vertebrae to be positively correlated with numbers of dorsal and of anal rays, and for the numbers of vertebrae

TABLE VII. Correlation between numbers of dorsal rays, and of anal rays, and vertebrae in *Reinhardtius hippoglossoides*. Based on a single collection of a single year-class, 76–103 mm in standard length, from Greenland, at 69°30′N., 56°32′W.

	Vertebrae				Vertebrae				
Dorsal rays	60	61	62	63	60	61	62	63	Anal rays
90	..	1	..	..	..	1	..	..	66
91	1	2	1	..	..	..	..	..	67
92	..	5	2	..	1	1	..	..	68
93	..	1	2	..	..	5	3	..	69
94	..	3	3	..	..	7	5	..	70
95	1	5	4	..	..	8	6	..	71
96	..	4	4	..	1	3	3	2	72
97	..	5	3	2	..	2	5	..	73
98	..	2	4	..	..	9	8	..	74
99	..	6	3	..	..	3	1	1	75
100	1	1	5	..	1	1	..	..	76
101	..	4	2	..	..	1	2	..	77
102	..	3	2	..	..	1	..	..	78
103	..	..	..	1	..	1	2	..	79
104	..	..	..	..					
105	..	..	1	..					
r = +0.18 (±0.11)							r = +0.12 (±0.10)		
90–97	2	26	19	2	2	25	17	2	66–72
98–105	1	16	17	1	1	18	18	1	73–79
Chi-square (2 × 2) = .60							Chi-square (2 × 2) = .64		

to differ in a parallel fashion when races or taxa differ in the number of dorsal and anal rays, it is surprising to discover an average difference in vertebral numbers between the Pacific and Atlantic materials, which show virtually no difference in ray numbers. We note also that the material from Sakhalin seems to be characterized by a relatively high average number of vertebrae coupled with low rather than, as would be expected, high average number of dorsal and anal rays. These observations led us to check the correlation between numbers of vertebrae and dorsal rays, between numbers of vertebrae and anal rays, and between numbers of dorsal and anal rays. For this purpose, to avoid differences related to locality or to age groups, we utilized a single large collection of young specimens 76–103 mm in standard length from Greenland, at 69°30′ N. Lat., 56°32′ W. Long. We do find for the 83 specimens counted, that the positive correlation is of very low order and definitely untrustworthy between numbers of vertebrae and dorsal rays ($r = +0.18 \pm 0.11$) and between numbers of vertebrae and anal rays ($r = +0.12 \pm 0.10$) (Table VII). The positive correlation between numbers of dorsal and anal rays (Table VIII), however, is strong and very significant, as was expected ($r = +0.58 \pm 0.07$).

In line with expectation (meristic correlations in fishes were generalized by Hubbs and Hubbs, 1954), the numbers of precaudal and caudal vertebrae, which are the anterior and posterior divisions of a linear series, are negatively correlated ($r = -0.49 \pm 0.08$) (Table IX).

TABLE VIII. Positive correlation between numbers of dorsal and anal rays in *Reinhardtius hippoglossoides*. Based on a single collection of a single year-class, 76–103 mm in standard length, from Greenland, at 69°30′N., 56°32′W.

	Anal rays													
Dorsal rays	66	67	68	69	70	71	72	73	74	75	76	77	78	79
90	..	..	..	..	1	..	..	..	..	..	..	..	..	..
91	1	..	1	..	1	1	..	..	..	..	..	..	..	..
92	..	..	1	3	2	1	..	..	..	..	..	..	..	..
93	..	..	..	1	2	..	..	..	..	..	..	..	..	..
94	..	..	..	1	..	4	1	..	..	..	..	..	..	..
95	..	..	..	..	4	2	1	1	1	..	..	..	..	1
96	..	..	..	2	1	1	..	3	1	..	..	..	..	..
97	..	..	..	..	..	2	3	1	3	..	..	..	..	..
98	..	..	..	..	..	..	1	1	3	..	..	1	..	..
99	..	..	..	1	..	2	..	1	3	1	..	1	..	..
100	..	..	..	..	..	1	2	..	2	1	1	..	..	..
101	..	..	..	..	1	..	..	..	3	1	1	..	..	..
102	..	..	..	..	..	..	..	..	1	1	..	1	1	1
103	..	..	..	..	..	..	..	..	..	1	..	..	..	..

$r = +0.58(\pm 0.07)$

TABLE IX. Negative correlation between numbers of precaudal and caudal vertebrae in *Reinhardtius hippoglossoides*. Based on a single collection of a single year-class, 76–103 mm in standard length, from Greenland, at 69°30′ N., 56°32′W.

	Caudal vertebrae		
Precaudal vertebrae	43	44	45
17	3	18	11
18	26	28	2

$r = -0.49(\pm 0.08)$

SYSTEMATIC CONCLUSIONS

The preceding analyses of inter-ocean and intra-ocean variations of *Reinhardtius hippoglossoides*, in both morphometric and meristic characters, provide no confirmation of previous opinions that this species is divisible into species or subspecies. What average differences do exist, most notably in the number of vertebrae, are indicated to be on the race, less than subspecies, level.

The Greenland halibut thus becomes another example of a species exhibiting an amphiboreal distributional pattern (i.e. occurring in the North Atlantic and North Pacific, but absent in the intervening Arctic Ocean). It perhaps is unique among amphiboreal forms in not exhibiting significant morphological differentiation at the subspecies or species level between the representatives in the two oceans. Since the species has a center of abundance far to the north in each ocean, it is plausible to assume a continuous range during the last Interglacial Period, and possibly even during the Postglacial hypsithermal period.

The very limited differentiation, if any, within either ocean may reflect the population structure, as deciphered by the Danish, Soviet, and Japanese fishery scientists. The species seems to find its main habitat in far-northern boreal waters, where reproduction is indicated to take place in deep water. The sparse southern populations appear to be made up of non-breeding expatriates from the far north. As such, they should not be expected to exhibit different characters.

ACKNOWLEDGMENTS

In determining the status and variation of this wide-ranging species we are indebted to a number of colleagues for the loan of material or for information, or both. Dr Jørgen Nielsen, of the Universitetets Zoologiske Museum, København, Denmark, provided many data and specimens from Greenland and the Eastern Atlantic, and Mr P. J. Whitehead, of the British Museum (Natural History), made measurements for us of Atlantic material. Material from the eastern Canadian Arctic and Atlantic has been made available by Dr M. J. Dunbar, of McGill University; by Mr Donald E. McAllister, of the National Museum of Canada; by Dr Giles W. Mead and Mrs Myvanwy M. Dick, of the Museum of Comparative Zoology, Harvard University; and by Dr Leonard P. Schultz, of

the United States National Museum. Dr Tokiharu Abe, of the University of Tokyo and the Tokai Regional Fisheries Research Laboratory, and Mr Kiyu Kobayashi, Dr Tatsuji Ueno, and Mr Koji Abe, of Hokkaido University, were particularly helpful in providing material and data from Japan and the Okhotsk Sea, to complement collections in the Institute of Fisheries, the University of British Columbia, from Okhotsk and Bering Seas. Mr Clifford H. Fiscus provided data on the occurrence of the species in a fur-seal stomach, from Bering Sea. Mr E. A. Best and Mr John E. Fitch, of the California Department of Fish and Game, provided specimens and data from California. Mr W. I. Follett generously supplied data on specimens from California in the California Academy of Sciences (the two known additional examples from the Californias are in the collection of the Scripps Institution of Oceanography). To all of these individuals and to the administrative authorities of their institutions go our grateful thanks.

The technical assistance of Mr Keith W. Radford and Mr John A. Bollinger, of Scripps Institution, and of Mr Andrew L. Hamilton and Mrs Johanne Hagen of the University of British Columbia, is much appreciated. Mrs Laura C. Hubbs has aided in the analysis of the data and has extensively helped in the preparation of this report.

REFERENCES

Note.—Literature cited only in the synonymy for the Pacific Ocean population is not entered here, nor has any effort been made to collect references to the Atlantic Ocean stock.

ABE, TOKIHARU. 1963. Unusual occurrences of several species of boreal, amphipacific and bathypelagic fishes in Sagami Bay and adjoining waters during the first half of 1963, a cold-water season in southern Japan. *Bull. Tokai Regional Fish. Res. Lab.*, **37**: 27–35.

BEST, E. A. 1963. Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), added to California fauna. *California Fish and Game*, **49**(3): 213–214.

BOYAR, H. C. 1964. Occurrence of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in shallow waters in the Gulf of Maine. *Copeia*, 1964 (1): 232–233.

DODIMEAD, A. J. 1961. Some features of the upper zone of the sub-Arctic Pacific Ocean. *Bull. Intern. N. Pac. Fish. Comm.*, No. 3, pp. 11–24.

DODIMEAD, A. J., F. FAVORITE AND T. HIRANO. 1963. Review of oceanography of the subarctic Pacific region. *Bull. Intern. N. Pac. Fish. Comm.*, No. 13, pp. 1–195.

DUNBAR, M. J., AND H. H. HILDEBRAND. 1952. Contribution to the study of the fishes of Ungava Bay. *J. Fish. Res. Bd. Canada*, **9**: 83–128.

H[oek], P. P. C. 1904. Catalogue des poissons du Nord de l'Europe, avec les noms vulgaires dont on se sert dans les langues de cette région. *Conseil Intern. Exploration Mer, Publ. Circonstance*, **12**: 1–75.

HUBBS, CARL L., AND LAURA C. HUBBS. 1945. Bilateral asymmetry and bilateral variation in fishes. *Papers Michigan Acad. Sci., Arts and Letters*, **30**: 229–310.

1954. Data on the life history, variation, ecology, and relationships of the kelp perch, *Brachyistius frenatus*, an embiotocid fish of the Californias. *California Fish and Game*, **40**: 183–198.

ISHIKAWA, C., AND K. MATSUŪRA. 1897. Preliminary catalogue of fishes including Dipnoi, Cyclostomi and Cephalochorda in the collection of the Natural History Department, Imperial Museum, Tokyo. 64 pp.

JENSEN, AD. S. 1935. The Greenland halibut (*Reinhardtius hippoglossoides* (Walb.)) Its development and migration. *Mem. Acad. Roy. Sci. et Lettres, Danemark, Sec. Sci.*, (9) **6**(4): 1–32.

JORDAN, D. S., AND J. O. SNYDER. 1901. Descriptions of nine new species of fishes contained in museums of Japan. *J. Coll. Sci., Imp. Univ., Tokyo*, **15**: 301–311.

MIKAWA, MASAO. 1963. Ecology of the lesser halibut, *Reinhardtius hippoglossoides matsuurae* Jordan and Snyder. *Bull. Tohoku Regional Fish. Res. Lab.*, **23**: 1–43.

MUSIENKO, L. N. 1954. Molod kambal (sem. Pleuronectidae) dalnevostochnykh morei SSSR. *Trudy Instituta Okeanologii*, **11**: 62–131.

NORMAN, J. R. 1934. A systematic monograph of the flatfishes (Heterosomata). Vol. 1, Psettodidae, Bothidae, Pleuronectidae. British Museum, London. 459 pp.

PERTSEVA-OSTROUMOVA, T. A. 1961. Razmnozhenie i razvitie kambal. *Izd. Inst. Okean. Akad. Nauk.* 484 pp.

RASS, T. S. 1955. Geograficheskoe rasprostranenie ryby i drugikh promyslovykh zhivotnykh Okhotskogo i Beringova morei. *Trudy Instituta Okeanologii*, **14**: 1–120.

TANAKA, SHIGEHO. 1918. Twelve new species of Japanese fishes. *Zool. Mag.*, **30**(356): 223–227. [In Japanese]

1931. On the distribution of fishes in Japanese waters. *J. Fac. Sci., Imp. Univ., Tokyo*, Sec. 4, **3**(1): 1–90.

VERNIDUB, M. F., AND K. I. PANIN. 1937. Nekotorye dannye o sistematicheskom polozhenii i biologii tikhookeanskogo predstavitelya *Reinhardtius* Gill. *Uch. Zapiski Leningr. Gos. Univer., Serv. Biol.*, **15**: 250–272. [German summary]

WELANDER, A. O., D. L. ALVERSON, AND P. BERGMAN. 1957. Rare fishes from the eastern North Pacific Ocean. *Fisheries Res. Papers, Washington Dept. Fish.*, **2**(1): 60–66.

APPENDIX

RECORD OF SPECIMENS AND CHARACTERS USED IN THIS INVESTIGATION

Below is given a record of the basic material for the preceding account of the distribution, variation, and systematics of *Reinhardtius*. Each lot of specimens utilized is accorded a separate entry, in the following order: clockwise from central Japan around the North Pacific to extreme northern Mexico; then, from north to south, first in the western, and finally in the eastern, Atlantic.

Each entry gives, in sequence:

1. The name of the institution holding the specimen or series (with the name abbreviated as indicated below).

2. The catalogue number, or for some lots, the field number.

3. In parentheses, the number of specimens used, and the size or size range, expressed as the standard length, in millimetres.

4. The data, with latitude and longitude where given, the depth, and other particulars (with measurements converted where need be into the metric system).

5. The characters used—parts measured and structures counted, indicated by abbreviations listed. The subscript numbers affixed to the abbreviations indicate the number of specimens utilized (this number is omitted when there is only one specimen in the lot and when the entire series has been counted or measured). When the counts and/or measurements have been made by others than ourselves or our technical assistants who are trained in our methods, the person who kindly provided the data is identified (in parentheses).

INSTITUTION MAINTAINING MATERIAL LISTED BELOW[5]

Abe, collection of Dr Tokiharu Abe, of Tokyo University and Tokai Regional Fisheries Research Laboratory, Tokyo, Japan.
EC, Institute of Fisheries, the University of British Columbia, Vancouver, Canada.
BM(NH), British Museum (Natural History), London, England.
CAS, California Academy of Sciences, San Francisco, California.
FFUH, Faculty of Fisheries, University of Hokkaido, Hakodate, Japan.
MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
NMC, National Museum of Canada, Ottawa.
SIO, Scripps Institution of Oceanography, University of California, San Diego; La Jolla, California.
SU, Division of Systematic Biology, Stanford University, Stanford, California.
USNM, United States National Museum (Natural History), Washington, D.C.
UZMK, Universitetets Zoologiske Museum, København (Copenhagen), Denmark.

ABBREVIATIONS FOR COUNTS AND MEASUREMENTS LISTED FOR EACH ENTRY[6]

A, anal rays
C, caudal rays (principal)
D, dorsal rays
MC, all meristic counts
P, pectoral rays, both sides
PL, pectoral rays, left side
PR, pectoral rays, right side
P′, pelvic rays, both sides
P′R, pelvic rays, right side
R, gill-rakers, both sides.
RR, gill-rakers, right side.
V, vertebrae, separately listed for precaudal and caudal.
X, all measurements: standard length, head length, upper-jaw length, length and depth of caudal peduncle.

PACIFIC OCEAN

Japan

Abe '63-445 (1; 302 mm), Sagami Nada, 800 m off Manazuru Saki; to depth of 20 m; 12.7°C near bottom; April 8, 1963: MC (except V), X. Specimen reported by Abe (1963).

FFUH 13765-13768 (4; 287–308 mm), off Cape Esan [at east tip of Oshima Peninsula, at about 42°00′ N., 141°30′ E.]; depth 275 m; collected by Kiyoshi Hayashi September 21, 1957: MC (except R and V), X.

FFUH (15; 320–543 mm), off Kushiro, Hokkaido; depth 530–605 m; taken by commercial vessel *Kotohira Maru* January 26, 1964: A, D, and X (all by Dr Tatsuji Ueno and Mr Koji Abe, in field).

FFUH (5; 376–532 mm), off Kushiro, Hokkaido; depth 200–340 m; taken by commercial vessel *Kotohira Maru* December 19, 1963: A, D, and X (all by Dr Ueno and Mr Abe, in field).

Sakhalin Island (southern part)

FFHU 14022 (1; 268 mm), off Ton-nai [which is at 46°52′ N., 143°10′ E.], Terpeniye Bay; depth 110–120 m; taken by *No. 7 Matsuei Maru* June 23, 1955: MC, X.

FFHU 14211-12, 14214-15 (4; 172–210 mm), Terpeniye Bay; June 1955: MC, X.

FFHU 14083-85, 14142-44 (6; 169–237 mm), off Sakaehama [which is at 47°25′ N., 142°50′ E.]; depth 120–130 m; taken by *Hokuō Maru* June 22, 1955: MC, X.

---

[5]The co-operating personnel of these institutions are listed in the Acknowledgments.

[6]Methods of measuring and counting are detailed on pp. 1137–1147.

Okhotsk Sea

Abe '63-584 (1; 310 mm), off Wakkanai, at northwest tip of Hokkaido, from trawl fishery, usually operating at depths of less than 200 m; June 20–30, 1963: MC (except V), X.

BC 64-248 (21; 234–533 mm), at 52°31′ N., 155°43′ E.; depth 56 m; trawled September 25, 1961 by the *Myo-Yo Maru* (original nos. 1A + 5 + 10A): MC (except R), X.

BC 64-249 (7; 350–530 mm), at 52°40′ N., 155°47′ E.; depth 52 m; trawled August 20, 1960 by the *Myo-Yo Maru* (original no. 8): MC (except R), X.

BC 63-402 (2; 248–403 mm), at 52°30′ N., 155°10′ E. to 53°10′ N., 155°10′ E.; depth 70–100 m; trawled July 2–8, 1961 by the *No. 12 Mito Maru*; specimen nos. 380–381: MC (except R), X.

FFUH 7298 (1; 544 mm), at 52°45′ N., 155°15′ E.; depth 98 m; collected August 15, 1963 by Shin Okada on *Osho Maru*: A, C, D, PL, P′, X.

Northwest Pacific off eastern Kamchatka

BC 63-404 (3; 450–587 mm), at 49°30′ N., 156°40′ E.; trawled October 1–10, 1961 by the *No. 31 Shôshin Maru*; specimen nos. 568–570: MC (except R), X.

BC 63-403 (20; 385–607 mm), from 49°40′ N., 156° E. to 50°30′ N., 175°20′ E.; trawled October 1–6, 1961 by the *No. 28 Shôshin Maru*; specimen nos. 515–534: MC (except R), X.

BC 63-405 (2; 283–562 mm), from 51°30′ N., 158° E. to 53° N., 160° E.; trawled October 17–28, 1961 by the *No. 12 Mito Maru*; specimen nos. 838–839: MC (except R), X.

Northwest Bering Sea

BC 64-246 (10; 438–662 mm), at 60°54′ N., 179°44′ W.; depth 330–390 m; trawled September 23, 1961 by the *Ten-Yo Maru* (original number 24B): MC (except R), X.

BC 64-247 (1; 516 mm), at 60°57′ N., 179°26′ W.; depth 260–380 m; trawled October 1, 1961 by the *Ten-Yo Maru* (original numbers 25A and 26A): MC (except R), X.

Central and Eastern Bering Sea

BC 63-401 (1; 445 mm), at 57°58′ N., 172°21′ W.; trawled June 6, 1961 by the *Kôyô Maru*; original number 195 (G): MC (except R), X.

BC 62-562 (7; 105–229 mm), about 185 km north of the Pribilof Islands; 58°33′ N., 170°12′ W.; trawled July 17, 1961 by the *John R. Manning* (of the United States Bureau of Commercial Fisheries): MC (except R), X.

BC 64-250 (about 500 young; 20 saved), collected by Clifford H. Fiscus August 24, 1963 from stomach of one fur seal taken about 93 km north-northeast of St. Paul Island, where the depth is 70 m: no counts or measurements.

BC 62-565 (1; 221 mm), about 139 km east of St. George Island; 56°38′ N., 167°34′ W.; trawled July 21, 1961 by the *John R. Manning*: MC (except R), X.

South of Tip of Alaska Peninsula

BC 62-550 (1; 446 mm), at 53°38′ N., 164°58′ W.; trawled August 30, 1961 by International Pacific Halibut Commission, on the *Morning Star*: MC (except R and V), X.

California

SIO 63-1088-64A (1; 548 mm), off Trinidad Head, California, on loran bearings 2H3-2250 to 2365, at a depth of 143–156 m [ca. 41°03′ N. to 41°10′ N., 124°20′ W.]; trawled June 14, 1963 by Mr Clifford Smith on trawler *Anna W.*; secured through Mr E. A. Best and Mr John E. Fitch, California Department of Fish and Game: MC (except R), X.

CAS 27029 (1; 379 mm), landed at Fort Bragg, California, in 1962 (from otter-trawl fishery extending from extreme southern Oregon to central California); secured by Mr E. A. Best, California Department of Fish and Game: MC (V by Mr W. I. Follett), X.

CAS 27030 (1; 421 mm), from otter-trawl fishery extending from extreme southern Oregon to central California; recovered December 11, 1962 at A. Paladini Fish Co. at Fort Bragg, California, by California Department of Fish and Game (secured by Mr Best): MC (except R; V by Mr Follett), X.

CAS 27031 (1; 510 mm), from same fishery; recovered in February or March 1963 at same fish company in Fort Bragg; collected by Dan Gotshall; donated by Mr Best: MC (V by Mr Follett), X.

SU 62133 (1; 581 mm), presumably off or near northern California, found July 6, 1963 on the fillet line of A. Paladini Fish Co. at Fort Bragg, California; obtained by Mr Best, California Department of Fish and Game: A, D, P, P′, X (all by Mr Best).

CAS 26921 (1; 558 mm), Gulf of the Farallones (roughly 38° N., 123° W.), off central California, in 91 fathoms or less; delivered to A. Paladini Fish Co. at Fort Bragg, California: MC (except D, uncountable due to injury; V by Mr Follett), X. Specimen secured by Mr Best, California Department of Fish and Game, and reported by him (1963: 213–214, fig. 1). Mr W. I. Follett informs us that this specimen contained in its stomach a Pacific tomcod, *Microgadus proximus* (Girard) 175 mm in total length (CAS 27078).

Extreme Northern Baja California, Mexico

SIO 62-249-64A (1; 638 mm), Baja California, Mexico, 8 km south of the United States–Mexico border, at a depth of 14.5–16.5 m, by Dominick Ghio; caught in a halibut net May 9, 1962: MC, X.

ATLANTIC OCEAN

Western Greenland

USNM 39748 (1; 149 mm), Greenland; from University Museum, Copenhagen; original number 48; entered October 5, 1888: P, PR, R, X (caudal peduncle only).

UZMK P 852605-08 (4; 200–245 mm), at 78°14′ N., 74°10′ W.; depth 672 m; August 8, 1928: A, D, PR, P′R, and X (by Dr Jørgen Nielsen).

UZMK P 852601-04 (4; 225–267 mm), at 77°28′30″ N., 68°27′ W.; depth 875 m; August 6, 1928: A, D, PR, P′R, and X (by Dr Nielsen).

UZMK P 852588-94 (7; 141–418 mm), at 75°29′ N., 62°30′ W.; depth 820 m; July 31, 1928: A, D, PR, P'_1, $P'R_6$, and X (by Dr Nielsen).

UZMK P 852609 (1; 158 mm), at 70°51′ N., 52°01′ W.; depth 733 m; September 15, 1928: A, D, PR, P′R, and X (by Dr Nielsen).

UZMK No. 54 (1; 121 mm), at Umanak; November 26, 1917: X (by Dr Nielsen).

UZMK (88; 76–103 mm), at 69°30′ N., 56°32′ W.; depth 202 m; otter trawl: D_{13}, A_{31}, PL_{81}, PR_{13}, V_{18}, X_{12}.

USNM 48848 (1; 427 mm), Jacobshavn, Greenland; P. S. Sorensen; entered June 29, 1898: MC (except V), X.

UZMK Nos. 23-24 (2; 131–132 mm), Jacobshavn; November 28, 1911: X (by Dr Nielsen).

UZMK No. 27 (1; 154 mm), at 68°28′ N., 54°27′ W.; depth about 360 m; August 18, 1908: A, D, PR, P′R, and X (by Dr Nielsen).

UZMK No. 101 (1; 137 mm), Holsteinsborg, Ikertok Fjord; depth about 240 m; August 13, 1935: X (by Dr Nielsen).

UZMK No. 108 (1; 179 mm), at 66°06′ N., 54°27′ W.; depth about 150 m; August 28, 1908: X (by Dr Nielsen).

UZMK No. 83 (1; 117 mm), harbor at Kangamiuts; September 18, 1916: A, D, PR, P′R, and X (by Dr Nielsen).

UZMK Nos. 129 and 136 (2; 244 and 345 mm), at 65°03′ N., 54°16′ W.; depth 80–120 m; June 7, 1909: X (by Dr Nielsen).

UZMK No. 53 (1; 599 mm), Lichtenau Fjord; 1914: X (by Dr Nielsen). Listed as a reversed specimen.

UZMK No. 81 (1; 107 mm), Lichtenau Fjord; taken at surface, June 11, 1914: X (by Dr Nielsen).

UZMK No. 86 (1; 171 mm), Angmasivik, Lichtenau Fjord; December 4, 1922: X (by Dr Nielsen).

UZMK Nos. 44 and 80 (2; 213 and 104 mm), harbor at Sydprøven, 60°27.5′ N., 45°34′ W.; September 21, 1914 and hand-taken January 10, 1936: X (by Dr Nielsen).

UZMK VII and XXVI (2; 572 and 566 mm), Sydprøven, 60°27′ N., 45°34′ W.; May 4, 1921: X (by Dr Nielsen). No. VII listed as a reversed specimen.

Arctic Canada

NMC 60-46 (1; 64 mm), Watts Bay, south-central Frobisher Bay, southeast Baffin Island, Franklin District, Northwest Territories; 62°39′ N., 66°51′ W.; depth 14–18 m; fish apparently stunned; taken July 21, 1952 by hand, on rising tide, near waterfall, where salinity was considerably influenced, on *Calanus* Expedition (station 403, F-2): RR (by Mr Donald E. McAllister), V, X.

NMC 59-403 (1; 76 mm), northeast Ungava Bay, Quebec, at Forbes Sound, about 2 km southwest-by-south of Port Burwell; 60°23.5′ N., 64°52′ W.; depth 91–128 m; beam-trawled June 30, 1949, probably on rock, on *Calanus* Expedition (station 102, B-1-1949): RR (by Mr McAllister), V, X.

Labrador

USNM 177629 (2; 79–105 mm), Hebron Fjord, Labrador; Drs Malcolm S. Gordon and Per F. Scholander, on *Blue Dolphin*, Cruise No. 12 (original no. MSG67), July 11, 1954: MC (except V), X.

NMC 63-132 (1; 195 mm), about 74 km off the eastern tip of Labrador; 52°05′ N., 54°26′ W.; depth 183 m; otter-trawled May 25, 1963 by Stanley W. Gorham on Cruise 70 of the *A. T. Cameron* (station 502, set 119): RR (by Mr McAllister), V, X.

NMC 63-133 (1; 430 mm), about 93 km off the eastern tip of Labrador; 52°01′30″ N., 54°11′00″ W.; depth 229 m; otter-trawled May 25, 1963 by Mr Stanley W. Gorham on Cruise 70 of the *A. T. Cameron* (station 503, set 120): V, X.

Newfoundland

NMC 63-151 (1; 154 mm), about 72 km east of the northern tip of Newfoundland, at 51°27′45″ N., 53°52′20″ W.; depth 320 m; otter-trawled May 31, 1963, on sand, mud, and gravel, by Mr Stanley W. Gorham on Cruise 70 of the *A. T. Cameron* (station 527, set 144): RR (by Mr McAllister), V, X.

NMC 63-156 (1; 101 mm), Bonavista Bay, about 13 km northwest of Cape Bonavista; 48°45′20″ N., 53°13′15″ W.; depth 183 m; otter-trawled June 2, 1963, on mud and stones, by Mr Stanley W. Gorham on Cruise 70 of the *A. T. Cameron* (station 535, set 152): RR (by Mr McAllister), V, X.

USNM 38097 (1; 342 mm), off Newfoundland, at Albatross Station 2697, at 47°40′00″ N., 47°35′30″ W.; depth 377 m; August 12, 1888; beam trawl: M, MC (except C and V).

Grand Banks

NMC 62-125 (1; 501 mm), at 45°30′00″ N., 48°19′00″ W.; depth 320 m; otter-trawled September 17, 1961, on sand and mud, by Mr Stanley W. Gorham on the *A. T. Cameron* (field no. G-14, set 409): RR (by Mr McAllister), V, X.

USNM 24716 (1; 327 mm), at 44°59′ N., 52°40′ W.; depth 366 m; Capt David Campbell; original no. 590; October 1879: MC (except V), X.

USNM 22881 (2; 414–415 mm), at 44°23′ N., 53°25′ W.; depth 366 m; G. W. Scott; original no. 290; catalogued May 21, 1879: R_1, PR_2, $P'R_1$, X_2.

NMC 62-130 (1; 102 mm), at 43°37′00″ N., 48°51′ 10″ W.; depth 274 m; otter-trawled September 19, 1961 on bottom of white sand and some mud, by Mr Stanley W. Gorham on the *A. T. Cameron* (field no. G-21, set 416): RR (by Mr McAllister), V, X.

Vicinity of Georges Bank

MCZ 38458 (2; 289–401 mm), at 42°42′ N., 63°47′ W.; 658–677 m; W. C. Schroeder, on *Cap'n Bill II*, Sta. 165; July 12, 1953: MC, X.

MCZ 38459 (1; 407 mm), at 42°38′ N., 64°10′ W.; 841–869 m; W. C. Schroeder, on *Cap'n Bill II*, Sta. 169; July 13, 1953: MC, X.

MCZ 37804 (1; 340 mm), at 42°20′ N., 65°03′ W.; 713–805 m; July 28, 1952: MC, X.

MCZ 37793 (1; 356 mm), at 42°18′ N., 65°04′ W.; 567–622 m; July 28, 1952: MC, X.

MCZ 38692 (1; 346 mm), at 40°55′ N., 66°20′ W.; 924–1097 m; June 26, 1954: MC, X.

Iceland

BM(NH) 1926.2.17.1-2 (2; 460 and 365 mm), off Siglu Fjord, north coast of Iceland; depth 460 m; collected by Dr Vilhelm Ege, on the *Dana*: A, D, and X (by Mr Peter J. Whitehead). Reported also by Norman (1934: 290).

BM(NH) 1924.11.14.1 (1; 445 mm), 22 km off Siglu Fjord; collected by Dr Johannes Schmidt, on the *Dana*: A, D, and X (by Mr Whitehead). Reported also by Norman (1934: 290).

Bear Island, south of Spitzbergen

BM(NH) 1932.10.29.1 (1; 358 mm): X (by Mr Whitehead).

Europe

UZMK 130[x] (1; 610 mm), Vordø, northern Norway: X (by Dr Jørgen Nielsen).

BM(NH) 1924.1.14.1 (1; 612 mm), southwest of Ireland, at 52°30′ N.; depth 311 m; collected by Dr W. M. Tattersall: X (by Mr Whitehead). Reported also by Norman (1934: 290).

Distribution of Introduced Marine Mollusca in British Columbia Waters[1]

By D. B. Quayle

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

The distribution of a number of species of lamellibranchs and gastropods that have been introduced into British Columbia waters largely as a result of oyster cultural operations is discussed. The dispersal routes and barriers are indicated in relation to known hydrographic conditions and circulation patterns. The problems of spawning, larval movements, metamorphosis, and spat survival are examined.

The introduced species that are discussed are *Crassostrea gigas, Mya arenaria, Venerupis japonica, Ocenebra japonica, Teredo navalis, Nassarius obsoletus, Purpura clavigera, Urosalpinx cinerea* and *Batillaria cumingi.*

INTRODUCTION

The fairly extensive literature on dispersal and subsequent distribution of exotic species has been brought together and analysed by Elton (1958), who stated (p. 100) "the greatest agency of all that spreads marine animals must be the business of oyster culture". The truth of this statement is probably nowhere better exemplified than on the west coast of North America as a result of the development of the culture of the Japanese oyster, *Crassostrea gigas*, and of the Atlantic oyster, *Crassostrea virginica*. In British Columbia alone more than a dozen well-known alien species have been involved as a result of oyster cultural operations and there are probably others. These species have been recorded briefly by Carl and Guiget (1958) for British Columbia and by Bonnot (1935), Hanna (1939), Kincaid (1949), and Ricketts and Calvin (1952) for the United States. However, dispersal methods and routes as well as the present distributional patterns of some of these species in British Columbia waters are of sufficient interest to warrant a more detailed account.

OYSTER CULTURE IN BRITISH COLUMBIA

The only indigenous oyster in British Columbia is the small native oyster, *Ostrea lurida* Carpenter (called the Olympia oyster in the United States). Natural beds of considerable size existed originally (Stafford, 1915; Elsey, 1933), and the early oyster industry carried on its business essentially as a fishery rather than as a culture and the beds gradually became depleted. At present *O. lurida* has no commercial importance in British Columbia.

[1]Received for publication May 13, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

The Atlantic oyster, *Crassostrea virginica* Gmelin, was introduced into the Pacific coast waters of the United States as early as 1870, first into San Francisco Bay and later into other areas, notably Willapa Harbour (or Shoalwater Bay as it was then called) in Washington (Smith, 1896). Reproduction occurred briefly in both these areas but breeding populations did not become permanently established. The species was introduced into British Columbia waters at the turn of the century and in 1906 three or four carloads were planted in Boundary Bay and Esquimalt Harbour. Originally, only seed oysters were brought in but high mortality soon caused a change to mature oysters which were merely relaid until required by market. Here, too, mortality was high and the margin of profit low. After 1912, a few carloads a year were planted and this ceased about 1936. However, Elsey (1933) records natural seeding of *C. virginica* in the estuaries of the Serpentine and Nicomekl Rivers in Boundary Bay. It was possible to find a few naturally spatted Atlantic oysters on the tidal flats of Boundary Bay 10–15 years ago, but this is no longer so. However, a small population attached to the tidal gates in the Nicomekl River still exists.

During the decline in abundance of the native oyster in the period between 1925 and 1930, the Japanese oyster, *Crassostrea gigas* (Thunberg), later known as the Pacific oyster, made its appearance. Trial shipments from Japan proved successful and by 1935 annual importations of considerable size were being made into British Columbia.

The seed is collected in Japan on oyster shell cultch and shipped across the Pacific as deck cargo in wooden boxes containing about 4 ft^3 of shell. Initially there was little inspection for pests and in Japan the seed was packed directly from the water into the wooden cases. Consequently it was often well laden with fouling organisms. Crevices and umbonal regions of the mother shells frequently contained mud, an ideal medium for the transport of many invertebrate species such as those listed by Kincaid (1949). A major pest introduced in this way was the oyster drill, *Ocenebra japonica* (Dunker), which became so well established in several areas of Washington State it soon constituted a serious threat to the well-being of the industry. As a result, a thorough inspection system was developed in order to prevent, as far as possible, widespread imports of both drills and other pests. Severe washing of the seed before packing is now accepted practice and the opportunity for fouling organisms to accompany seed is very much reduced. However, by the time the inspection system (now supervised in Japan by United States biologists) was introduced and perfected, any Japanese species associated with oysters and capable of gaining a foothold in western North American coastal waters had already done so.

These, then, were the processes that resulted in some very striking faunal changes in British Columbia coastal waters, particularly in the Strait of Georgia.

INTRODUCED SPECIES

Crassostrea gigas

Initial plantings of Pacific oysters were concentrated in Ladysmith Harbour, Pender Harbour, Baynes Sound, and Boundary Bay (Fig. 1). Previous to 1932

there had been no significant breeding of Pacific oysters anywhere in British Columbia, but a major spawning and successful spatfall in that year have been described by Elsey (1935) and Elsey and Quayle (1939).

The 1932 spawning originated 1½ miles from the head of Ladysmith Harbour on 10 acres of ground containing an estimated 5 million oysters. This was the only Pacific oyster planting in the Stuart Channel area at that time, so it could be safely assumed that this compact group of spawners in Ladysmith Harbour formed the source of spat distributed throughout the area. Because of this and

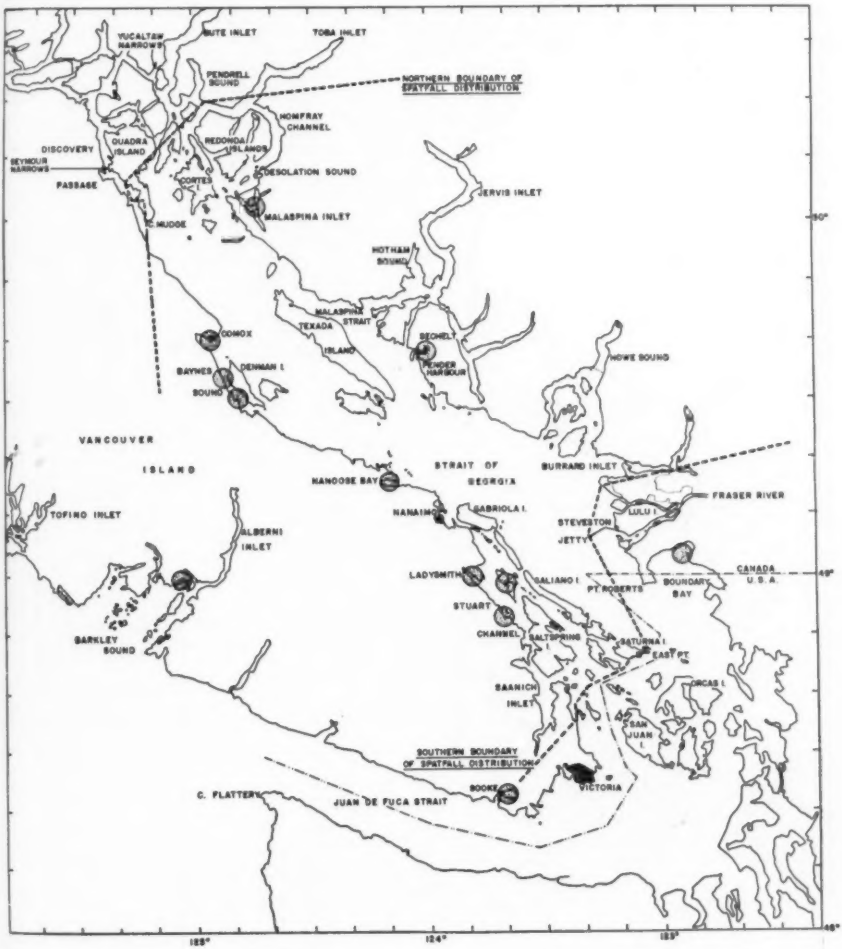


FIG. 1. Oyster growing areas in British Columbia (stippled circles) with northern and southern limits of the distribution of the 1958 Pacific oyster spatfall.

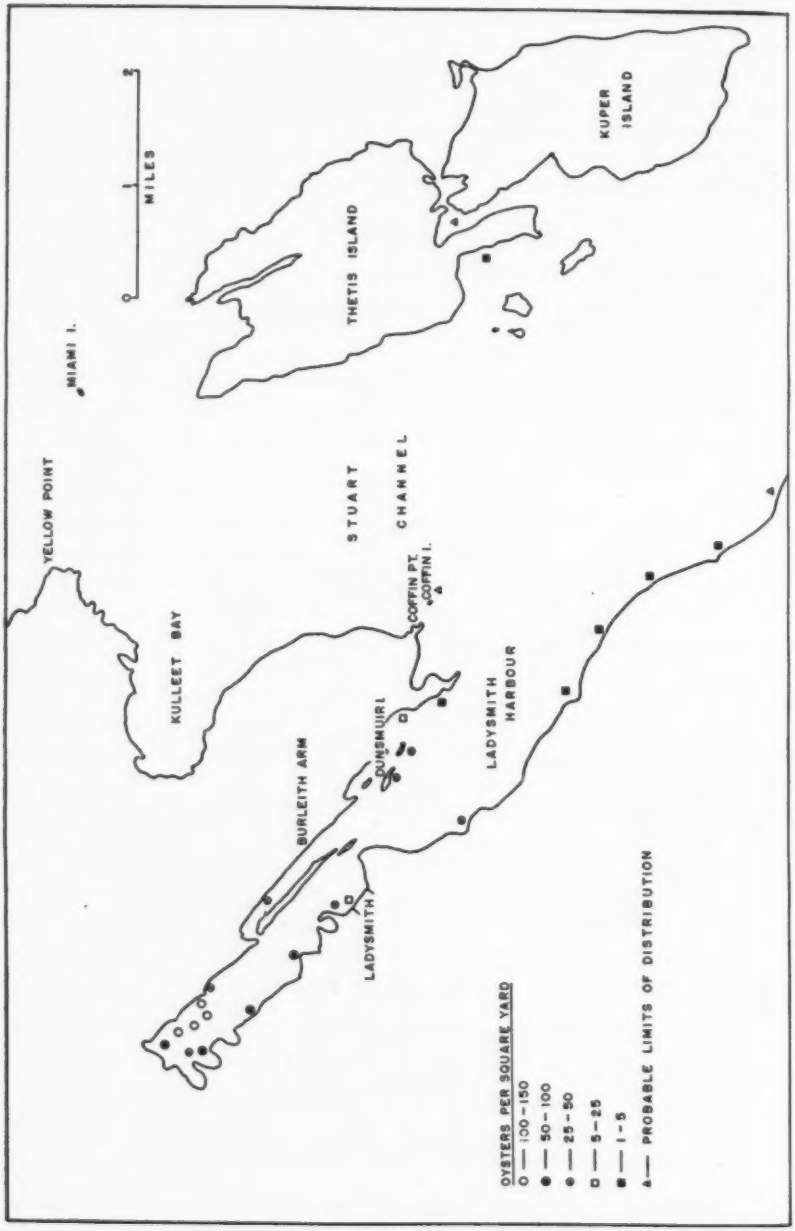


FIG. 2. Distribution of the 1932 Pacific oyster spatfall. After Elsey (1935).

the fact that the dispersal pattern of the larvae could be readily observed from oysters on natural cultch in the intertidal area this occasion provided a unique opportunity to study the dispersal of a lamellibranch larva from a known spawning source. The survey to determine the distribution of the 1932 set was carried out in 1934 when the spat were 3 or more inches in length. Probable limits of distribution, up to 10 miles from the centre of spawning, are shown in Fig. 2. Floating cultch in the vicinity of oyster beds collected 13 spat per Pacific oyster shell (700 per m^2) while areas along the adjacent shore caught 150 per m^2.

Two further breedings, both of commercial magnitude, occurred in Ladysmith Harbour in 1936. There was still no concentration of oysters outside

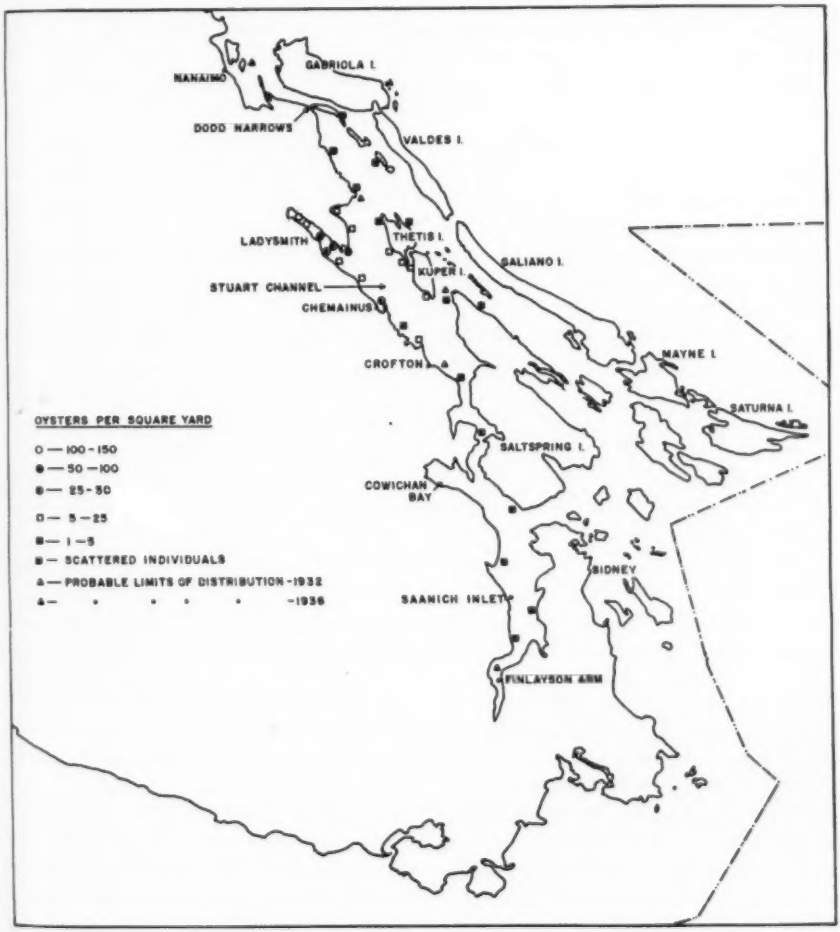


FIG. 3. Distribution of the 1936 Pacific oyster spatfall. After Elsey and Quayle (1939).

FIG. 2. Distribution of the 1932 Pacific oyster spatfall. After Elsey (1935).

Ladysmith Harbour large enough to provide the nucleus of a significant breeding population so this area could also be taken as the origin of all the 1936 spat in the Gulf Islands area. One of these spawnings was the result of artificially stimulated spawning (Elsey, 1936). Floating oyster-shell cultch from these sets collected 0.5 spat per cm^2 and on bottom oyster-shell cultch 0.25 spat per cm^2 while the adjacent shore at the 5–7-ft tide level caught 200 spat per m^2 (Elsey and Quayle, 1939).

The spat from these later breedings which could be readily distinguished from those of 1932 were found 20 miles north and 35 miles south of the spawning area (Fig. 3). Doubtless the actual distribution was somewhat greater. The free-swimming period of larvae contributing to these sets was between 18 and 22 days. The ebb tide, which flows southeasterly in Stuart Channel at a maximum rate of 1–3 knots, is stronger and of longer duration than the flood. In addition, prevailing winds during summer are from the northwest, and no doubt contributed to the greater southerly dispersal.

In 1942, a further major breeding in Ladysmith Harbour was apparently responsible for a heavy set at Crofton, a point 10 miles to the south. Presumably this must have resulted from a particular set of current conditions during the larval period for the set in Ladysmith Harbour in 1942 was no greater than that in 1936. The circumstances prevailing at the time of breeding influence to a large extent distribution of pelagic larvae, as demonstrated by Orton (1937) and Coe (1953).

In addition to the breeding in Ladysmith Harbour in 1942 there was widespread reproduction in practically all major oyster-growing areas in the Strait of Georgia (Fig. 1) for the first time since these grounds were planted. In Ladysmith Harbour itself, successful breeding is sporadic and there have been only 7 commercial sets in the last 23 years, although in most intervening years there was light spatting. Similar inconsistent breeding of *C. gigas* occurs in most oystering areas of Washington State indicating the species is probably at or near its geographical breeding limit.

Two planted oystering areas where breeding occurred in 1942 were Pender Harbour and Baynes Sound, located near the northern end of the Strait of Georgia, one on each side (Fig. 1). Later, wild oysters were to be found on most islands in the Strait of Georgia and in mainland sounds wherever suitable setting areas were to be found — both to east and west of Pender Harbour and Baynes Sound. These are the only sources from which these wild oysters could have originated. According to Tully and Dodimead (1957), circulation in the Strait of Georgia results from flood waters from the south being displaced northward, principally on the mainland side to the northern end with the northward movement weak or nonexistent on the Vancouver Island side. The flood tide from the north is strongest on the Vancouver Island side and creates a southward flow. This probably inhibits the flood from the south, creating a continuity of flow northward along the mainland side of the Strait. On the mainland side north of the Fraser River the southward ebb movement is slight if any and the northward ebb movement increases toward the northern passages. Along the Vancouver Island

side the southward ebb is the dominant flow. These movements are shown in Fig. 4, according to Waldichuk (1957), who confirms this general picture of an anti-clockwise circulation from several sources of information.

Considering this current pattern and speed, and an estimated larval period of about 20 days, Pender Harbour was the most likely source of the main body of oyster larvae that reached the northern part of the Strait through Malaspina Strait and on to the region of Cortes Island where local currents would continue

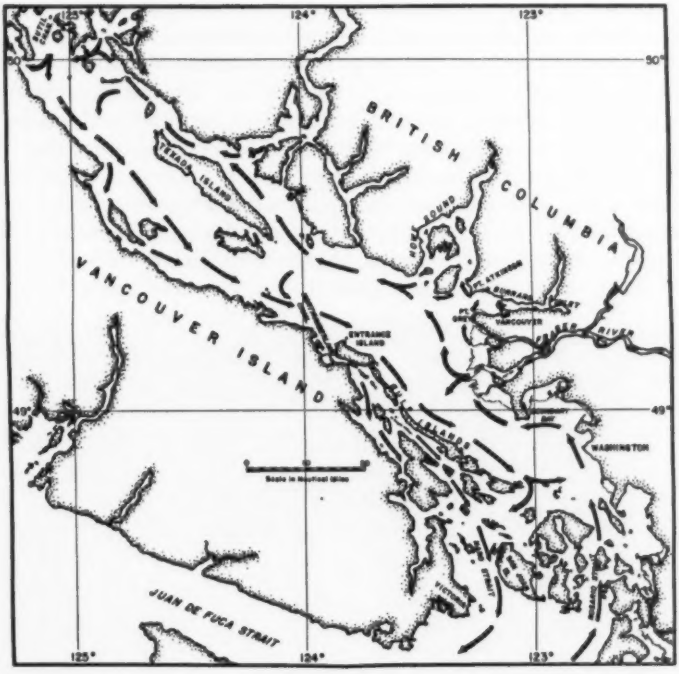


FIG. 4. Surface current patterns in Georgia Strait. After Waldichuk and Tabata (1955).

dispersal among the islands and into mainland inlets. Baynes Sound would then be the source of larvae for the spatfalls along the Vancouver Island shore between there and the Strait of Georgia side of the Gulf Islands. The striking feature of the final distributional pattern was the penetration of enough larvae into inlets such as Jervis, Malaspina, and Pendrell Sound (Fig. 1) to form significant breeding populations. According to oceanographers (Tully, 1949; Pickard, 1953) the net water movement, particularly of surface waters, is out of these channels, although at the time of year in question, July and August, net outflow is probably close to minimum due to low river discharge. In addition, however, there are counter currents beneath or lateral to the outgoing currents.

In deep inlets without a sill, such as Pendrell Sound, the main tidal current effects are apparently felt only in the deep waters. Wind-driven currents may also have considerable effect, particularly in narrow waterways. The current situation in many of these inlets is complex and still not well understood.

These widespread spatfalls were of particular interest because of the establishment of breeding populations in Hotham Sound (offshoot of Jervis Inlet) and especially in Pendrell Sound. In this latter area there exists a unique set of hydrographic conditions for Pacific oyster breeding (Quayle, MS, 1957). This fortuitous introduction created a situation of considerable economic and biological importance. The Pacific oyster is now the dominant intertidal organism in that area with 50 miles or so of rocky shoreline virtually covered with oysters between the 0- and 10-ft tide marks (Fig. 5). Since 1949 when Pendrell Sound was first investigated, breeding has occurred annually without fail, often with extraordinary intensity. Setting up to 10 or more spat per cm^2 is common and as many as 500 per cm^2 have been recorded.

As soon as the oyster seed producing potential was realized, a government reserve was placed on the area, prohibiting acquisition of leases, but permitting seed collection. At any rate, there is no growing (culture) ground in the area because of steep rock shores. Consequently no outside seed has been introduced

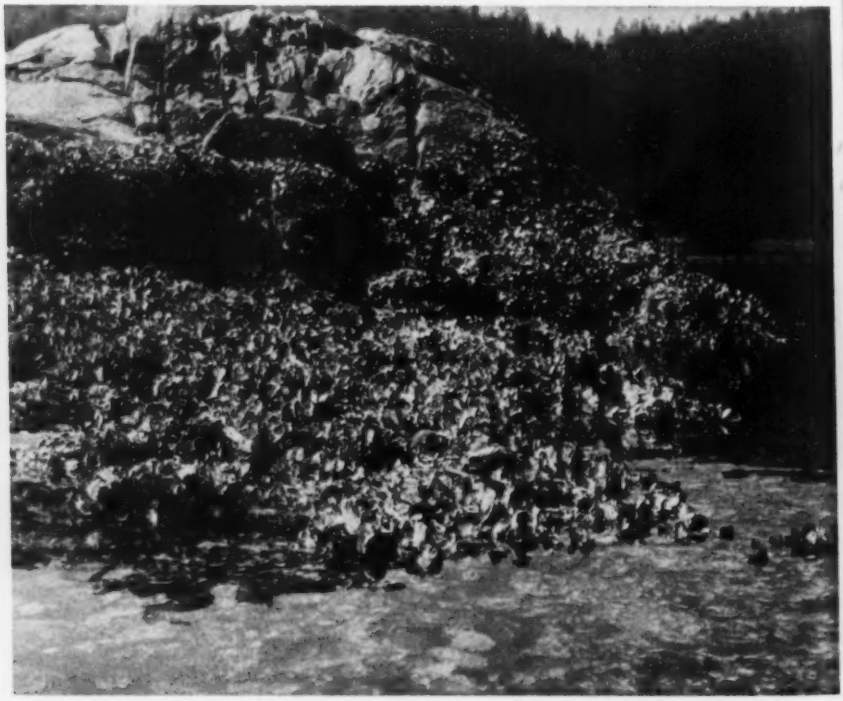


FIG. 5. Photograph of intertidal area in Pendrell Sound showing Pacific oysters.

into the Sound, beyond the relatively few larvae that may have penetrated in 1958 from other oyster areas. Therefore an isolated, nearly pure line, oyster stock is being developed and it will be of interest in years to come to compare specific characteristics of Pendrell Sound oysters with those of parent stock from Miyagi Prefecture in Japan. Since, up to the present time, culture of Pacific oysters on the west coast of North America has been predicated on annual or fairly frequent importation of seed from Japan, no other pure line stock has been developed as far as is known.

Although Pacific oysters are grown between Morro Bay, California (latitude 35°N) and Ketchikan, Alaska (55°N), breeding occurs only between Willapa Harbour (46°N) and Pendrell Sound (50°N). The source of seed in Japan in Miyagi Prefecture lies at 36°N Latitude. It is probably only in Pendrell Sound that consistent high-level annual breeding takes place, indicating the importance of local conditions and the fortuitous combination of circumstances that permitted establishment of a breeding stock there.

In 1958, apparently due to favourable weather conditions, there was a second widespread breeding in the Strait of Georgia on a scale exceeding by far that of 1942. Heavy setting occurred along the mainland shore as far south as the Fraser River and on the Vancouver Island side to the lower end of the Gulf Islands. Actual limits of distribution are shown in Fig. 1 and an example of the intensity of set is demonstrated in Fig. 6, showing the south

FIG. 6. Photograph showing Pacific oysters on rocky shore, Brandon Island, Departure Bay, near Nanaimo, B.C. (Photograph by C. Morley).

shore of Brandon Island in Departure Bay. This breeding was an excellent demonstration of the way in which breeding intensity affects distribution with high larval abundance leading to wide distribution. Time element is involved for high larval abundance is usually associated with prolonged breeding, for optimum conditions for both factors are the same. Also, optimum conditions, particularly high temperature, are associated with a short larval life (18 days at 22°C and 30 days at 18°C; Quayle, 1959), with increased opportunity for survival, but decreased opportunity for dispersal. The Pacific oyster, however, differs from the Atlantic oyster in that spawning peaks are generally more definite. In Pendrell Sound, except in very favourable years, there are usually quite discrete larval broods that may be readily identified. In 1942 a lower level of larval abundance, as indicated by the setting intensity near the sources of larvae was correlated with a much reduced distribution as compared to 1958.

In 1961, a third widely-spread breeding occurred comparable in magnitude to that of 1942.

Mya arenaria

It appears to be the general, although not unanimous, opinion that the lamellibranch *Mya arenaria* Linnaeus was introduced to the Pacific coast of North America from the Atlantic coast during the last century.

Introduction was by means of plantings of the Atlantic oyster, *Crassostrea virginica*, into San Francisco Bay. Newcombe (1875) described it as *Mya hemphillii*, and Stearns (1881) and Smith (1896) stated *Mya arenaria* was abundant in San Francisco Bay subsequent to 1874. Newcombe (1893) indicated it was a frequent fossil in boulder clay. Taylor (1895), unable to find living specimens on beaches near Victoria prior to 1888, found it abundant in 1890 and later traced it to the north end of Vancouver Island. Presumably the *Mya* mentioned by Taylor (1895) must have originated in Puget Sound where Smith (1896) indicated they were planted from Shoalwater Bay (now Willapa Harbour) where the species had become abundant by 1884. The movement of the species from San Francisco to Willapa Harbour is also described by the latter author. Thompson (1914), who recorded it from southern British Columbia in 1912 but not from the Queen Charlotte Islands, stated "it may be simply a matter of time before it reaches the Islands (Queen Charlotte Islands)".

In 1939, beds of *M. arenaria* were found by the author in estuaries in Masset Inlet and later in Naden Harbour on the north coast of the Queen Charlotte Islands (Fig. 7). Most of the east and west coasts of the Islands have been examined but the only other area where *M. arenaria* has been found is Rennell Sound on the west coast of Graham Island (Fig. 7) although suitable habitats occur throughout all of these areas. On the mainland, the species occurs at least as far north as Juneau, Alaska. Since it does not occur on Moresby, the southern island of the Queen Charlotte Islands, the obvious dispersal route would be along the mainland shore to the Alaska border and from there to the north end of Graham Island, across Dixon Entrance. The direct distance between the islands of the mainland shore and Masset Inlet, the nearest suitable habitat,

is about 50 miles. In Hecate Strait proper, the flood tide sets northward and the ebb southward in a simple reversing tidal system. In northern Hecate Strait, however, there is a region of confused and rotary tide currents (MacKay, 1954). At the southern end of Hecate Strait currents are quite weak. In summer, winds are generally from the north and less than 20 mph, while in winter they are from the south, varying from light to gale force. Summer surface temperatures in the area are between 13 and 14°C with relatively high salinities (31–32‰). According to the Canadian Hydrographic Service in Pacific Coast Tide and Current Tables (1962), the flood tide coming in through Dixon Entrance on reaching the northern end of Hecate Strait divides at a point midway between Rose Spit and Dundas Island where the weaker part of the current sets northward past Dundas Island. According to Trites (1956) more than 70% of Skeena River water moves northward and leaves Chatham Sound through Dundas and

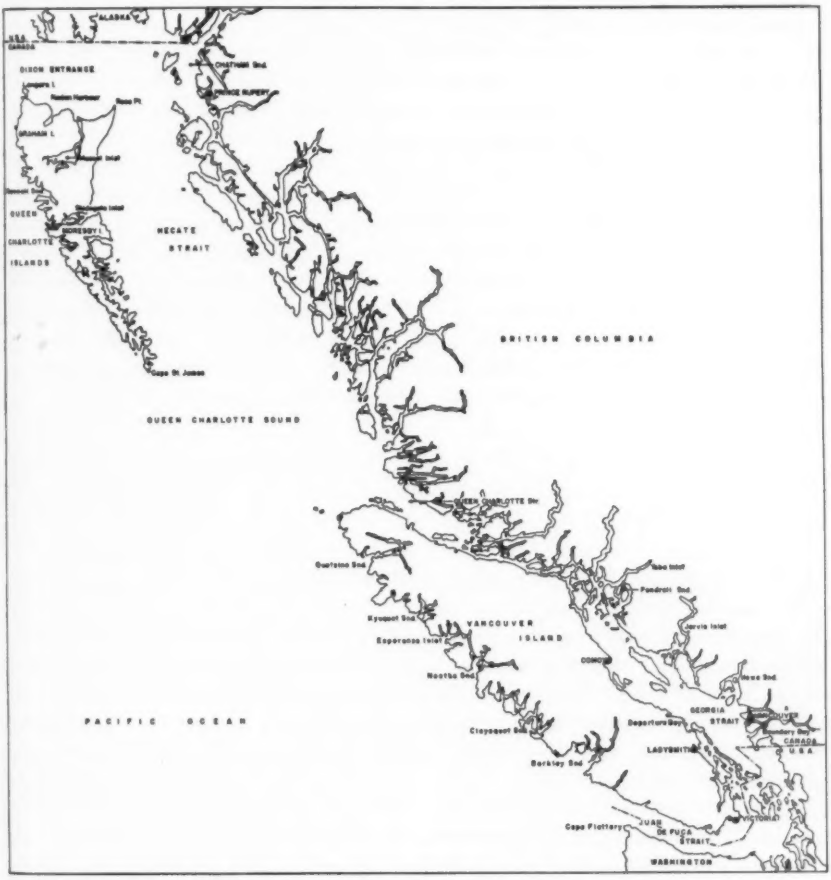


FIG. 7. Map of British Columbia coast showing place names mentioned in the text.

Hudson Passage. Crean (MS, 1963) has described two major features of water movements in Dixon Entrance. There is a net northward flow out of Chatham Sound past Dundas Island and westward past the southernmost islands of Alaska. Some of this water is held within the general area and moves to form a vortex between these islands and Rose Spit. This system has been confirmed by model studies (Bell, MS, 1963). It would appear from the above that this anti-clockwise circulation could account for the transport of larvae from the mainland area of Chatham Sound. Recently, *M. arenaria* has been located on the Alaskan islands bordering Dixon Entrance. The distance from these islands to Masset Inlet by the circulation postulated would be approximately 50 miles. On the basis of a study of copepod distribution, Cameron (1957) postulated an eastward flow of surface water in Dixon Entrance adjacent to Graham Island as demonstrated by drift bottle data (Thompson and Van Cleve, 1936). Near Langara Island at the northwest corner of Graham Island the flood tide attains a speed of 5 knots on spring tides and 3 knots on the ebb. At summer surface-water temperatures pertaining in Dixon Entrance (14°C) and length of larval life of *M. arenaria* at this temperature (14 days at 10–12°C, Loosanoff (1943)), the transport could have been readily accomplished.

Since *M. arenaria* does not occur anywhere on Moresby Island as far as is known, or on the east coast of Graham Island, it appears that transport of larvae across Queen Charlotte Sound or the southern part of Hecate Strait has not been possible. This premise is supported by the drift bottle data of Thompson and Van Cleve (1936) and the lemon sole studies of Ketchen (1956).

Thus, *M. arenaria* has been able to move northward along the British Columbia coast from Victoria to the Queen Charlotte Islands, a distance of between 500 and 600 miles in the period between 1890 and some time prior to 1939, for when the species was discovered in Masset Inlet, the size and abundanc indicated the population had been established for some time.

Venerupis japonica

The Japanese little neck (or Manila) clam, *Venerupis japonica* (Deshayes), was first observed in Ladysmith Harbour in 1936. By 1941 this species had dispersed so rapidly and reproduced so abundantly it had entered the commercial clam catch along with the native little neck, *Protothaca staminea* Conrad. By this time also it had becone the dominant lamellibranch species on many beaches in the Stuart Channel area.

Introduction was undoubtedly brought about by transportation of young individuals, several millimeters in length, in cases of Japanese oyster seed. The young clams would be either attached to cultch shells by byssal connection or in mud clinging to shells especially in the umbonal cup. By the time the oyster seed inspection system had become properly organized and working, *Venerupis japonica* was firmly established. Consequently, opportunities for introduction of this species were much greater prior to 1940 than they are now. Nevertheless, the numbers involved in the introduction must have been very small and at the time they were discovered in Ladysmith Harbour in 1936 relatively few adult specimens could be found.

By 1942, *V. japonica* occurred in Saanich Inlet, Departure Bay, and Pender Harbour (Fig. 1). In 1944, it was found in Nanoose Bay and Lasqueti Island, and was thus distributed over a distance of about 80 miles. Neave (1949) stated that in Departure Bay only two seasons of spawning were required to make this species the dominant lamellibranch in the area. *V. japonica* became widely known throughout Puget Sound at about the same time and later became common and abundant in all parts of the Strait of Georgia as well as on the west coast of Vancouver Island between Barkley Sound and Esperanza Inlet.

Venerupis japonica became established as an abundant species with extraordinary rapidity, and optimum conditions must occur on the North American west coast, for it breeds in San Francisco Bay and Humboldt Bay in California, in Willapa and Grays Harbour and Puget Sound in Washington as well as in British Columbia. The species has also a wide range in Japan, being found between 25° and 45°N latitude, a distribution similar to that of *Crassostrea gigas* (23–47°N). In British Columbia it has not yet extended beyond about 50°N. In the Strait of Georgia, as with the Pacific oyster, the tidal passages at the north, Seymour Narrows, Okisollo Channel, and Yuculta Rapids, apparently present a temperature barrier, for the species does not occur northward of these areas. July and August surface-water temperatures at the entrance to Seymour Narrows at Cape Mudge average about 14°C while at the southern entrance to the Strait of Georgia at East Point on the southern tip of Saturna Island mean July–August water temperature is only 11.5°C (Pacific Oceanographic Group, MS, 1963). Along the west coast of Vancouver Island, however, where average summer surface temperatures rarely exceed 14°C, *V. japonica* has been able to migrate from Barkley Sound, the only area where significant Japanese oyster seed plantings have been made, to as far north as Esperanza Inlet, a distance of about 80 nautical miles. For part of this distance there are protected channels where summer water temperatures are higher than those of the open ocean. There are actually only two open water stretches of about 20 miles each. Set of the current along the shore of the west coast of Vancouver Island is always northwestward (Tully, 1937; British Columbia Pilot, Vol. 1, 1959) with the strength varying between ½–2½ knots.

Ocenebra japonica

The Japanese oyster drill, *Ocenebra japonica* (Dunker), was introduced into Canadian and United States Pacific waters with the Japanese oyster as early as 1928 (Galtsoff, 1929). Because of predation by this drill and despite concerted attempts to combat it, some oyster grounds have been abandoned (Chapman and Banner, 1949) and seed mortality has been considerable on other grounds. Great effort has been expended in attempting to prevent further introduction from Japan and spread from areas where it has already become established.

Fortunately, *O. japonica* has no pelagic larval stage. According to Chapman and Banner (1949), females deposit an average of 25.3 egg cases each under aquarium conditions, and each case contains an average of 1543 eggs. However, only 2 or 3 of these eggs survive to hatch. Development in the egg case

takes up to 2 months in Ladysmith Harbour toward the end of the breeding season which lasts from about April to November. The young merely crawl out of the aperture at the top and on to the substratum which is usually on the underside of oysters, shells, or sunken wood debris. According to experiments by Chapman and Banner (1949) there is very little migration and in southern Puget Sound after a 10-year period, *O. japonica* was strongly localized and had not spread into adjoining oyster beds. Since that survey conducted in 1942, however, there was considerable dispersal in the next 10 years. General Order No. 249 of the State of Washington Director of Fisheries, dated 1950, lists 13 areas restricted because of pests, presumably the Japanese oyster drill, while Chapman and Banner (1949) list only 4 areas.

From two sites in British Columbia where the drill occurred in 1950, Boundary Bay and the head of Ladysmith Harbour, the species has now spread to Crofton, Thetis Island, Holland Bank in Ladysmith Harbour, Comox Harbour, and Henry Bay. However, only in Ladysmith Harbour, and at times in Boundary Bay, can it be considered a serious pest. The occurrence in Ladysmith Harbour can be attributed to direct importation from Japan while the infestation in Boundary Bay and possibly Comox is believed due mainly to oyster transplantation from Samish Bay in Washington in 1941. The other infestations have occurred because of inter-bed movement of oysters and equipment.

In Ladysmith Harbour where the drill had become relatively abundant by 1935, distribution within the harbour remained relatively unchanged until about 1955 indicating minimum migratory movement. During this time movement of oysters was entirely into the infested area but subsequent to about 1955 when some expansion in the industry took place, oysters were moved from infested grounds to formerly drill-free grounds. Figure 8 shows the difference in the distribution between 1950 and 1962.

All evidence points to the fact that distribution of *O. japonica* is likely to occur only by means of direct transfer either of egg cases or drills themselves. Accidental movement, as on driftwood, is apparently most unlikely, to judge from the static distribution pattern that occurred for many years in a very small area of Ladysmith Harbour.

Teredo navalis

The Atlantic shipworm, *Teredo navalis* Linnaeus, is well known on the Pacific coast due to the dramatic destruction of large numbers of untreated piling in San Francisco Bay during the period around 1920. This area was assumed to be the northerly limit of its distribution in the Pacific coast. In 1957, however, the writer found the species in Willapa Harbour, Washington, about 600 miles north of San Francisco Bay.

Prior to this, Brown (1951, 1952) reported *Teredo* sp. from Vancouver Harbour and nearby False Creek. Specific identifications were not made. Test block studies in Vancouver Harbour by the British Columbia Research Council beginning in 1950 and continuing until the present time have failed to show any other teredine borer but the indigenous *Bankia setacea* Tryon.

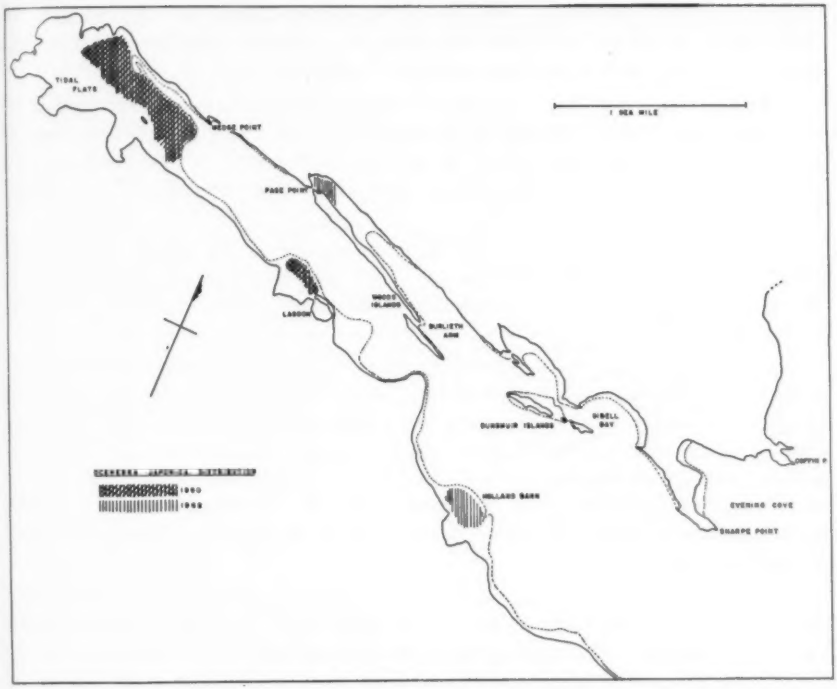


FIG. 8. Distribution of *Ocenebra japonica* in Ladysmith Harbour, B.C.

More recently, however (August 1963), in the course of investigations on the supposedly introduced crustacean wood borer, *Limnoria tripunctata* Menzies, in Pendrell Sound, *Teredo navalis* was found in considerable numbers. Ecologically, Pendrell Sound presents a suitable habitat for this species while Vancouver Harbour does not.

In recent years, Pendrell Sound has become a favourite visiting place for yachts from the United States and these could well have been the means of introduction of the species.

The presence of *Teredo navalis* in Pendrell Sound will require a thorough survey of the Strait of Georgia area to determine its distribution for it may be more widespread than is now indicated. If Pendrell Sound is the only locus of infection at the moment, its dispersal to other areas both by larval movement and by transport of the adults in wood is inevitable.

Doctor R. D. Turner, Museum of Comparative Zoology, Harvard University, kindly confirmed the identification of *Teredo navalis*.

Nassarius obsoletus

Another gastropod, the eastern mud snail, *Nassarius obsoletus* Say, was also introduced with the Atlantic oyster and has become well established in Boundary

Bay but, as far as is known, nowhere else in British Columbia. In the State of Washington, it occurs in Willapa Harbour, the site of extensive plantings of *C. virginica*, as well as in San Francisco Bay, California.

This species is a summer spawner and egg capsules have been taken in Boundary Bay during July. According to Scheltema (1962), egg capsules are laid at a temperature of 13–17°C but larvae do not emerge until temperatures (20°C) that will assure growth in the pelagic stages have been maintained for several days.

Temperature for optimum rate of development of the pelagic larva is at 24–25°C when the period is 17–18 days. Very slow development occurs between 15 and 20°C. Salinities of 15–20‰ mark the lower limit of tolerance for both larvae and adults.

A survey in June 1956 showed *Nassarius* to be concentrated in the corner of Boundary Bay between Crescent Beach and a point 2 miles to the northwest (Fig. 9), where it was actively breeding. Search to the south as far as Birch Bay or as far west as Tsawwassen failed to locate the species. In July 1963 another survey was made and the southerly limit of distribution was still located at the south end of the town of Crescent Beach. Distribution had extended northwestward a mile or two beyond the previous limit. Egg capsules occurred at this time also.

This is a very limited and static distribution for a species with a fairly long pelagic larval life and there must be an explanation. The substratum habitat beyond the confines of present distribution limits appears to be not too different from that within, although beyond Point Roberts to the west, wave action would probably be a limiting factor.

Waldichuk (1957, 1958) postulates a large counter-clockwise gyral in the area of southern Strait of Georgia, partly on the basis of drift bottle data and partly on other oceanographic information. Surface winds throughout the year (Harris and Rattray, 1954) also show a counter-clockwise circulation in southern Strait of Georgia with southeast winds blowing nearly directly into Boundary Bay both winter and summer. These characteristics of the area may tend to limit the degree of dispersal but it is doubtful if they would prevent it completely.

In the upper reaches of Boundary Bay (more properly, Mud Bay) summer temperatures range between 18 and 21°C (Elsey, 1933) and are attained chiefly through warming of extensive tidal flats. Salinities average about 25‰. However, only 4 or 5 miles away in Semiahmoo Bay (White Rock) the mean summer surface water temperature did not exceed 16°C in 1954, the only year in which complete records are available (Pacific Oceanographic Group, MS, 1954). Oceanographic stations (Pacific Oceanographic Group Data Record, MS, 1954) taken just outside the Bay area showed summer temperatures in the 15–17°C range with salinities below 20‰ at the surface.

In the light of Scheltema's (1962) data it would appear that the temperature and salinity regime outside the Bay proper may be sufficiently marginal either to cause immediate death to the larvae or to prolong the larval life only long enough

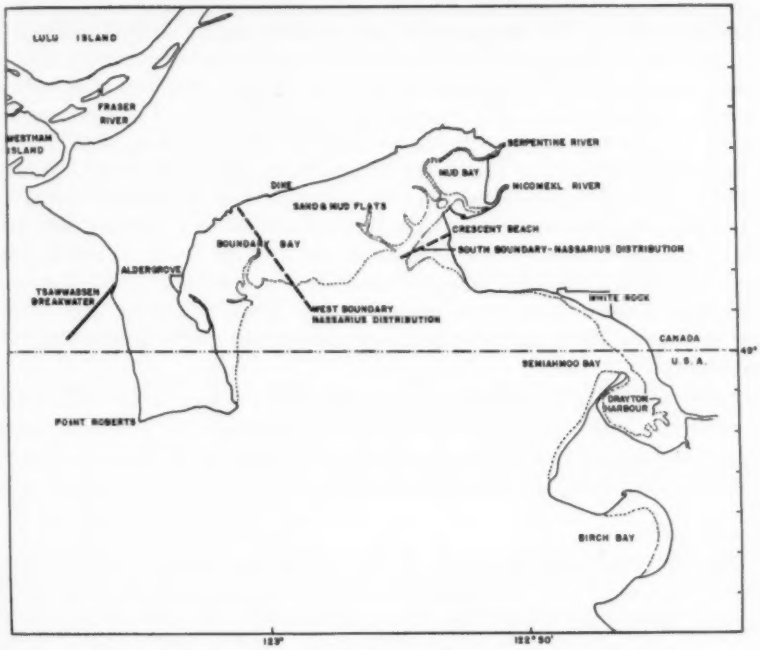


FIG. 9. Distribution of *Nassarius obsoletus* in Boundary Bay, B.C.

to allow them to be carried into even more unfavourable conditions. It is unexpected that this species, so successful and ubiquitous along the Atlantic coast of North America from the Gulf of St. Lawrence to northern Florida, should have such a very limited distribution in British Columbia in spite of quite a high population level within the confines of its area of occurrence.

Purpurx clavigera

Another Japanese species of oyster drill, *Purpura* (*Mancinella*) *clavigera* Küster (also known as *Thais tumulosa*), has been found in Ladysmith Harbour. During a drill survey there in 1951, most of a group of 63 specimens were collected from a small area of about 100 square yards, indicating a common origin. This was likely a single case of Japanese oyster seed, probably from a planting on this bed in 1948. At the time of discovery all were adults and several groups of egg capsules were found. The immediate area was thoroughly combed to find every last specimen, for this species has a free-swimming larva. If these were viable in British Columbia waters, dispersal of the species could conceivably have been widespread and rapid. No further specimens were found in Ladysmith Harbour and it has not been discovered elsewhere.

Urosalpinx cinerea

The eastern oyster drill, *Urosalpinx cinerea* Say, which was introduced into Boundary Bay with the Atlantic oyster, survived there but has not spread

beyond that area. The temperature and salinity regime in Boundary Bay is well within the limits required for breeding and development (minimum spawning temperature of 12–13°C (Galtsoff *et al.*, 1937; Cole, 1942) and the waters of Boundary Bay may reach 20°C or more for short periods). *U. cinerea* occurs in Atlantic waters with salinities that range between 15‰ or less up to 35‰. Summer salinities in Boundary Bay range from 23‰ to 30‰. However, *U. cinerea* is partially a subtidal animal but other than sloughs that occur at low tide, there is no suitable habitat for it below the zero tidal level in Boundary Bay where the bottom is pure sand. This is probably the limiting factor in preventing its spread beyond the tidal flat area of Boundary Bay proper. There has been a considerable movement of oystering equipment from Boundary Bay to other areas but except for a single record from Ladysmith Harbour none has been found elsewhere.

There appears to have been a general decline in the abundance of this species in recent years indicating that conditions for its existence are probably marginal and that renewal of stocks from additional plantings of Atlantic oysters were necessary to maintain significant population levels.

Batillaria cumingi

Probably the most abundant of the introduced gastropods is *Batillaria cumingi* (Grosse). This is a Japanese species and so far its distribution is associated directly with oyster beds that have been planted with Japanese oyster seed. Boundary Bay, Ladysmith, Crofton, Fanny Bay, and Comox are areas where this species is abundant. Its habitat is sand or relatively firm muddy bottom with maximum abundance at approximately the mid-point and higher in the intertidal zone. Numbers up to 80 individuals per square yard have been recorded. Nothing is known of the breeding habits of this species, but judging from its limited distribution it may have a larva with a short pelagic period, or without a pelagic life.

DISCUSSION

Since the distributional pattern of many marine invertebrates is based on success in spawning, larval movements, metamorphosis, and spat survival, a comment on these factors is pertinent to a discussion of the dispersal of introduced species.

Breeding

In a study of an introduced species, the first consideration is whether the temperature range is suitable for gonad development and eventually for spawning. Oyster seed which carried new species to British Columbia originated in Miyagi Prefecture in Japan. In Mangoku-ura Bay a water temperature of 20°C is maintained between May and October and over 25°C for at least July and August with a maximum at 30°C (Imai *et al.*, 1951). In contrast, Ladysmith Harbour, which is a protected harbour in the central Strait of Georgia, seldom reaches 20°C. The influence of temperature on breeding is shown in Fig. 10

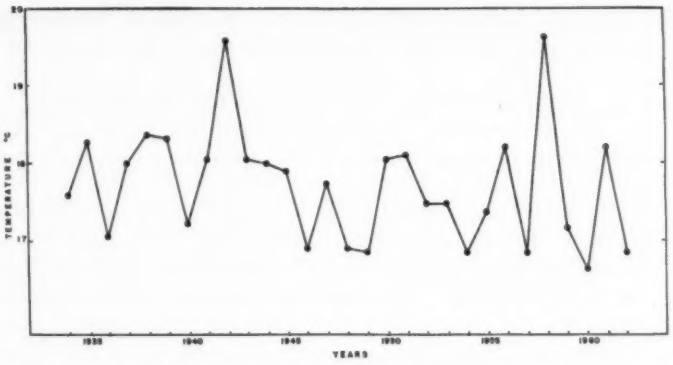


FIG. 10. Mean July–August surface water temperature at Departure Bay, B.C. Data from Hollister (MS, 1960).

where the temperatures in 1942 and 1958, the years of general breeding throughout the Strait, are compared to the 1935–58 means for the breeding months of July and August.

Gonad development and ripening in *C. gigas* takes place regularly, beginning in May and reaching maturity in late June in most years. However, as discussed by Smith (1953), ripening does not necessarily mean automatic release of gametes.

When first introduced into Ladysmith Harbour, *C. gigas* rarely spawned and stimulated spawning was resorted to (Elsey, 1936), and spatfalls were obtained by this method. It is possible that the species would not have become as securely established as it has without the continued replenishment of stocks by seed imports until the fortuitous occurrence of exceptional conditions suitable for successful breeding in 1942. Since about 1940, natural spawning has occurred in most years, though no doubt accidental stimulation of one sort or another occurs as growers break clusters and transplant oysters during summer. Nevertheless, there are still years when little or no spawning occurs on many cultivated beds in the Strait of Georgia as in, for example, 1953 and 1954 (Quayle, 1954a, 1954b). Prolonged periods of low water temperatures appear to be associated with this situation although there may be other factors. Non-release of gametes is not unique to exotic species for there is the example of the butter clam, *Saxidomus giganteus*, an indigenous and abundant species near the centre of its geographical range (Keen, 1937) at Seal Island near Comox in the Strait of Georgia. Here the last major spatfall occurred in 1935, a breeding which produced about 1000 tons of marketable clams on 10 acres of ground. At no time during the 3 years prior to 1940 and 6 years after 1948 and in several years since, did continuous gonad examination indicate a significant release of gametes. This has resulted in a very low level of reproduction, which has existed since 1935. Such a situation may be more common than is realized since breeding success of few species, other than those of economic importance, has been studied in detail for extended periods.

This could well be an important cause of fluctuating population size of many marine invertebrates. Another example is that of the wedge clam *Donax* in California (Coe, 1953).

Venerupis japonica, however, has shown remarkable facility in adapting itself to the new environment (particularly when compared with *C. gigas*), ripening and discharging sexual products with apparent regularity in spite of a very different temperature regime from that of its home waters. This is also true of *Ocenebra japonica* but not of another introduced Japanese lamellibranch, *Trapezium liratum* (Reeve), which has shown no sign of successful breeding in British Columbia, but it is not known whether this has been a problem of numbers, spawning, or larval survival. The Japanese flatworm, *Pseudostylochus ostreophagus* Hyman, has not "exploded" in British Columbia waters as it has at times in Puget Sound. The introduced parasitic copepod, *Mytilicola orientalis* (Mori), has apparently had little difficulty in maintaining breeding populations in the areas of introduction in British Columbia but has not so far attained epidemic proportions, and has not spread far beyond the original sites of infection in spite of availability of hosts. This situation, however, may change in the future. The wood borer, *Limnoria tripunctata* Menzies, believed to have been introduced from Japan, has proved to be very successful in some localities as shown by its frequent preponderance over the native species, particularly where water temperatures are higher than average. *Urosalpinx* and *Nassarius* have been able to produce gametes but environmental factors appear to limit abundance and dispersal. *Batillaria cumingi* has become well established, even prolific, on oyster grounds where Japanese seed oysters have been planted, but it has not spread far beyond the limits of seed plantings. *M. arenaria* has had no difficulty in breeding successfully in a wide variety of environments and temperature regimes.

Larval Survival

Unless time-consuming studies are made it is difficult to draw very firm conclusions on success of larval survival, beyond evidence supplied by the extent of annual settlements which can be misleading because of lack of knowledge of the number of larvae involved initially.

Most complete studies have, once again, been made on *Crassostrea gigas*, particularly in Pendrell Sound where a considerable number of larval broods over a period of time have been followed quantitatively from spawning to spatting. Grazing is said to be the major cause of decimating phytoplankton populations and there is every reason to believe this may apply to pelagic larvae, as suggested by Thorson (1950).

Quantitative estimates of larval populations from early-stage larvae to pre-setting in Pendrell Sound show survival levels of up to 2%, which must be considered quite high. Larval numbers from some spawnings have exceeded 400 per litre.

When an introduced species is, as in the case of this oyster, at or near the periphery of its geographic breeding range, larval survival may vary widely on the basis of temperature conditions alone. This is certainly so with *C. gigas*.

Attrition of a larval population on account of dispersal by currents may be important in that larvae may be carried from the near optimum conditions of the spawning site to the areas where lethal or marginal conditions occur. This is suggested by the presumed temperature barriers in the tidal passages, particularly in the southern and northern Strait of Georgia.

Pendrell Sound may represent an atypical situation, particularly in respect to predators of oyster larvae. There are virtually no planktonic predators other than a relatively small population of the ctenophore *Pleurobrachia bachei* which has been observed to catch oyster larvae. The main sessile predator is without doubt the adult oyster which is the dominant intertidal animal.

Metamorphosis

Thorson (1946, 1950) has discussed this problem in detail and has arrived at the conclusion that there are many species whose larvae are highly selective in respect to the substratum on which they settle or become attached, and are able to postpone metamorphosis if necessary. Wilson (1937, 1951, 1958) and others support this point of view.

Later, Thorson (1957, p. 485) agreed that "larvae may be forced to settle on a substratum that has few attractive qualities" and further (page 482) that "in certain cases the substratum may deceive the larvae and tempt them to settle on a bottom which will prove unfavourable to the adults." Smith (1953) also mentioned this possibility. Quayle (1952) indicated there may be some selection on the part of the larva of *Venerupis pullastra* (Montagu) but it is directed mainly to the immediate needs of larva and spat and not necessarily toward those of the adult. Consequently, mortality may occur, rather than prior to or at metamorphosis, during a period up to a year or so after, if the substratum chosen is not suitable for the growing animal.

The larvae of *C. gigas* are known to be able to exercise considerable selection in respect to the type of surface on which they will set (as, for instance, greasy or slick surfaces on some plastics), but there seems to be little choice as to where the surface is. By continuous examination of collectors during setting, *C. gigas* have been found to settle in quantity up to the level of the highest tide, but mortality ensued almost immediately at the higher tide levels because of desiccation. The main body of larvae of *C. gigas* in Pendrell Sound is concentrated at all stages of the tide, day or night, within 4 or 5 m of the surface yet the effective spatfall occurs from the zero tide level to less than 3 m above it.

Crassostrea gigas spat settles readily on almost any object, and bacterial or algal coverings are not necessary as indicated for some organisms by Zobell and Allen (1935). Clean, washed oyster shell exposed for 3 hr has collected up to 80 spat on one shell surface (50 cm^2).

Setting over a broad area with survival only in the restricted zone inhabited by adults must be common to many invertebrates.

No doubt there are all shades of ability to select substratum by invertebrate larvae and selectivity is likely variable even at specific levels.

Larval Movements

In addition to direct passive transport of lamellibranch larvae by currents, there is some evidence of limited vertical movement of the larvae themselves. Bousfield (1955) with *Balanus* larvae, and Nelson and Perkins (1931), Carriker (1951), Pritchard (1953), Manning and Whaley (1954) with the larvae of *Crassostrea virginica* have shown, to a certain extent, at least, that older stages tend to concentrate in the deeper strata of higher salinity in estuaries where two-layer systems exist (Pritchard, 1953). In addition, Yasuda (1952) describes tidal and diurnal changes in the vertical distribution of molluscan larvae at Maeshiba, Japan. Cahn (1951) states "indications are that the pelagic larvae of *Venerupis semidecussata* and other clam species are carried close to shore on the flood tide and they sink to the bottom when the tide slackens and begins to ebb." Quayle (1952) indicated diurnal changes in the vertical distribution of the larvae of *Venerupis pullastra* in Fairlie Channel, Scotland. Further studies by the same author on the larvae of the Pacific oyster, *Crassostrea gigas* (Quayle, MS, 1957), and of the shipworm, *Bankia setacea* (Quayle, 1959) in Pendrell Sound, British Columbia, also show these larvae to have limited vertical movements. Here (Pendrell Sound) *Crassostrea* larvae tend to remain above a fairly well-defined thermocline while *Bankia* larvae tend to remain below it. Isham *et al.* (1951), in studying the larvae of *Teredo pedicellata*, concluded that under natural conditions they will concentrate at the surface during darkness and during the day will be dispersed and tend to remain in deeper, less-illuminated waters.

Banse (1955), however, did not find diurnal vertical movements of larvae, particularly of polychaetes and echinoderms, in the Kieler Bucht.

Vertical movements of larvae, where they exist, have been shown to have considerable importance in dispersal of larvae and ultimate distribution of settled forms, particularly in two-layered systems or in others with wind-induced surface currents. Such currents occur in the Strait of Georgia where Waldichuk and Tabata (1955) have found that the wind effect on surface water movements is quite pronounced in regions removed from shore. Pacific oyster larvae are never very deep and even short vertical movements would bring them within the effect of surface currents for at least part of the day.

Banse (1956) suggests that the horizontal and vertical distribution of the larvae he investigated (mainly polychaete and echinoderm) is not dependent on any orientation of the animals but is governed by hydrographic events. The importance of the hydrographic situation no doubt supersedes any other factor with most planktonic organisms, the only exception being the most active swimmers and lamellibranch larvae cannot be counted among these.

Cole and Knight-Jones (1949) and Knight-Jones (1951) have demonstrated a group-spatting phenomenon in the European flat oyster, *Ostrea edulis*, both in tank and natural breeding. They term it "gregariousness" and tentatively explain it on the basis of chemical attraction. A similar phenomenon is observed in *Crassostrea gigas* and was most apparent when the distribution of the 1932 and 1936 spatfalls in Ladysmith Harbour were being studied. In areas 5–10 miles

from the centre of spawning there were found aggregations of spat separated by several hundred yards even though apparently identical setting areas occurred in the intervening areas. Similar situations were found in the Pendrell Sound area with distances between groups of spat sometimes measured in miles. Separated aggregations of the mussel, *Mytilus edulis* Linnaeus, also occur in the same area. In Pendrell Sound itself, in the very centre of the area of highest setting intensity, the tendency to aggregate has been observed. In this instance, with the plethora of chemical stimuli within the Sound, and outside, together with the great distances between aggregations, a "rafting" of the larvae by concentration through current action would be a more likely explanation than chemical stimuli. Whatever the reason, the end result is highly satisfactory for an oviparous marine animal with a long pelagic life.

Indeed, in the pelagic life of such larvae two opposing and necessary forces are at work. One is the *dispersal* effect of currents permitting the species to establish breeding populations in new areas (as in Pendrell Sound) or to maintain vegetative populations in old habitats (areas of the Strait of Georgia proper). The extensive literature on dispersal of planktonic indicator organisms is of interest in this connection. Another striking example is the dispersal of the immigrant barnacle *Elminius modestus* in the British Isles (Bishop, 1951; Crisp and Chipperfield, 1948).

Opposing the dispersal effect of currents is the *concentrating* effect of convergences and current eddies. The importance of this factor in bringing together sufficient individuals to permit successful breeding is apparent. Davis (1923) has described the dense concentrations of newly settled *Spisula subtruncata* on the Dogger Bank on the North Sea, and Orton (1937) has described the settlement of lamellibranchs due to current eddies. Turner (1953) has observed similar concentrations of adults, and Kellogg (1905) and Belding (1909) explain unique clam sets on the basis of this sort of mechanism.

So far, *C. gigas* has been contained within the Strait of Georgia proper. The tidal passages to the north and to the south, with their extreme turbulence and consequent maintenance of a year-round regime of relatively low temperature, have acted as barriers to further dispersal. As described previously, there have been, however, occasional and isolated breedings on the west coast of Vancouver Island in Barkley Sound, Sidney Inlet, Nootka Sound, and Kyuquot Sound. However, there has been little dispersal beyond the planting sites and as far as is known, no new breeding areas have been developed as a result of dispersal in this region.

The movement of *M. arenaria* northward along the coast of British Columbia is an excellent example of the "springboard" effect where larvae were dispersed, growth and breeding took place, and then another jump was made. Basic to this sequence of events are adequate breeding temperatures, and necessary along-shore currents with the proper directions for dispersal of the larvae. Then the concentrating effect of eddies and convergences form populations large enough to produce adequate numbers of larvae for maintenance or spread of the species.

Several authors (Johnson, 1939; Crisp and Southward, 1953, 1959; Knox, 1954) have discussed the dispersal of marine invertebrates in relation to the distance the larvae may be transported. In British Columbia, however, temperature appears to be more critical than distance in the dispersal of introduced forms.

REFERENCES

BANSE, K. 1955. Über das verhalten von meroplanktischen Larven in geschichtetem Wasser. *Kieler Meeresforsch.*, **2**: 188–200.

1956. Über den Transport von meroplanktischen Larven aus dem Kattegat in die Kieler Bucht. *Ber. Deut. Wiss. Komm. Meeresforsch.*, **14**: 2, 147–164.

BELDING, DAVID L. 1909. A report on the mollusk fisheries of Massachusetts. Commonwealth of Massachusetts, Boston.

BELL, W. H. MS, 1963. Hecate Model. *Annual Report, Fish. Res. Bd. Canada Pacific Oceanographic Group*, pp. 50–56.

BISHOP, M. W. 1951. Distribution of barnacles by ships. *Nature*, **167**(4248): 531–533.

BONNOT, P. 1935. A recent introduction of exotic species of molluscs into California waters from Japan. *The Nautilus*, **49**(1): 1-2.

BOUSFIELD, E. L. 1955. Ecological control of the occurrence of barnacles in the Miramichi Estuary. *Bull. National Museum of Canada*, No. 137, pp. 1–69.

BROWN, D. W. 1951. Fifth Progress Report on marine borer activity in test boards operated during 1951. William F. Clapp Laboratories, Inc., Duxbury, Mass.

1952. Sixth Progress Report on marine borer activity in test boards operated during 1952. *Ibid.*

CAHN, A. R. 1951. Clam culture in Japan. *U.S. Fish Wildlife Serv., Fishery Leaflet* No. 399, pp. 1–103.

CAMERON, F. E. 1957. Some factors influencing the distribution of pelagic copepods in the Queen Charlotte Islands area. *J. Fish. Res. Bd. Canada*, **14**(2): 165–202.

CANADIAN HYDROGRAPHIC SERVICE. 1959. British Columbia Pilot, Vol. 1, 6th ed., Dept. Mines and Tech. Surveys, Ottawa, 480 pp.

1962. Annual Tide Tables for the Pacific Coast of Canada, Surveys and Mapping Branch, Dept. Mines and Tech. Surveys, Ottawa.

CARL, G. C., AND C. J. GUIGUET. 1958. Alien animals in British Columbia. *British Columbia Provincial Museum, Handbook* No. 14, pp. 1–94.

CARRIKER, M. B. 1951. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. *Ecol. Monogr.*, **21**: 19–38.

CHAPMAN, W. M., AND A. H. BANNER. 1949. Contributions to the life history of the Japanese oyster drill, *Tritonalia japonica*, with notes on other enemies of the Olympia oyster, *Ostrea lurida*. *Washington State Dept. Fish. Biol. Bull.*, No. 49–A, pp. 169–200.

COE, W. R. 1953. Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents. *Ecology*, **34**(1): 225–229.

COLE, H. A. 1942. The American whelk tingle, *Urosalpinx cinera* (Jay), on British oyster beds. *J. Mar. Biol. Assoc. U. K.*, **25**: 447–508.

COLE, H. A., AND E. W. KNIGHT-JONES. 1949. The setting behaviour of larvae of the European flat oyster, *Ostrea edulis* L., and its influence on methods of cultivation and spat collection. *Fish. Invest. London*, Ser. 2, **17**(3): 1–39.

CREAN, P. B. MS, 1963. Oceanography of Dixon Entrance. *Annual Report, Fish. Res. Bd. Canada, Pacific Oceanographic Group*, pp. 47–50.

CRISP, D. J., AND P. M. J. CHIPPERFIELD. 1948. Occurrence of *Elminius modestus* (Darwin) in British waters. *Nature*, **161**(4080): 64.

CRISP, D. J., AND A. J. SOUTHWARD. 1953. Isolation of intertidal animals by sea barriers. *Nature*, **172**(4370): 208–209.

1959. The further spread of *Elminius modestus* in the British Isles to 1959. *J. Mar. Biol. Assoc. U.K.*, **38**(3): 429–437.

DAVIS, F. M. 1923. Quantitative studies on the fauna of the sea bottom. No. 1, Preliminary investigation of the Dogger Bank. *Fish. Invest. London*, Ser. 2, **6**(2): 1–54.

ELSEY, C. R. 1933. Oysters in British Columbia. *Bull. Biol. Bd. Canada*, No. 34, pp. 1–34.

1935. Distribution of oyster larvae. *Fish. Res. Bd. Canada, Pacific Prog. Rept.*, No. 22, pp. 19–20.

1936. Artificial stimulation of spawning in the Pacific oyster. *Ibid.*, No. 29, pp. 10–11.

ELSEY, C. R., AND D. B. QUAYLE. 1939. Distribution of oyster larvae from the 1936 spawning in Ladysmith Harbour. *Fish. Res. Bd. Canada, Pacific Prog. Rept.*, No. 40, pp. 8–10.

ELTON, C. S. 1958. The ecology of invasions by animals and plants. Methuen, pp. 1–181.

GALTSOFF, P. S. 1929. Oyster industry of the Pacific Coast of the United States. *Rept. U.S. Comm. Fish.*, Doc. 1066, App. 8, pp. 367–400.

GALTSOFF, P. S., A. H. F. PRYTHERCH AND J. B. ENGLE. 1937. Natural history and methods of controlling the common oyster drills (*Urosalpinx cinerea* Jay and *Eupleura candata* Jay). *U.S. Bur. Fish., Circular* 25, pp. 1–24.

HANNA, G. D. 1939. Exotic Mollusca in California. *Bull. Dept. Agric., State of California*, No. 28, pp. 298–321.

HARRIS, R. G., AND M. RATTRAY. 1954. The surface winds over Puget Sound and the Strait of Juan de Fuca and their oceanographic effects. *Univ. Washington Dept. Oceanography, Tech. Rept.*, No. 37, pp. 1–101.

HOLLISTER, H. J. MS, 1960. Classification of daily observations of seawater temperature and salinity on the Pacific Coast of Canada 1915–1959. *Fish. Res. Bd. Canada, MS Rep. (Oceanogr. Limnol.)* No. 68, 139 pp.

IMAI, TAKEO, *et al.* 1951. Ecology of Mangoku-ura Inlet with special reference to the seed-oyster production. *Sci. Rep. Res. Inst. Tohoku Univ.*, D-Vol. 1–2, pp. 137–156.

ISHAM, L. B., F. G. WALTON-SMITH AND V. SPRINGER. 1951. Marine borer attack in relation to conditions of illumination. *Bull. Mar. Sci. Gulf and Caribbean*, **1**(1): 46–63.

JOHNSON, M. W. 1939. The correlation of water movements and dispersal of pelagic larval stages of certain littoral animals, especially the sand crab, *Emerita*. *J. Mar. Res.*, **2**(3): 236–245.

KEEN, A. MYRA. 1937. An abridged check list and bibliography of west American marine Mollusca. Stanford University Press, Photolith, pp. 1–88.

KELLOGG, J. L. 1905. Conditions governing existence and growth of the soft-shell clam, *Mya arenaria*. *Report U.S. Comm. Fish and Fisheries* for 1903, **29**(4): 195–224.

KETCHEN, K. S. 1956. Factors influencing the survival of the lemon sole (*Parophrys vetulus*) in Hecate Strait, British Columbia. *J. Fish. Res. Bd. Canada*, **13**(5): 647–694.

KINCAID, T. 1949. Note on introduced Mollusca. Minutes of the Conchological Club of Southern California, No. 88, 1 p.

KNIGHT-JONES, E. W. 1951. Aspects of the setting behaviour of larvae of *Ostrea edulis* on Essex oyster beds. *Rapp. et Proc.-Verb., Cons. Int. Explor. Mer.*, **128**: 30.

KNOX, G. A. 1954. The intertidal flora and fauna of the Chatham Islands. *Nature*, **174** (4436): 871–873.

LOOSANOFF, V. L. 1943. Soft and hard clams of the Atlantic Coast of the United States. *U.S. Fish Wildlife Serv., Fishery Leaflet*, No. 13, 11 pp.

MACKAY, B. S. 1954. Tidal current observations in Hecate Strait. *J. Fish. Res. Bd. Canada*, **11**(1): 48–56.

MANNING, J. H., AND H. H. WHALEY. 1954. Distribution of oyster larvae and spat in relation to some environmental factors in a tidal estuary. *Proc. Nat. Shellfish Assoc.*, **45**: 56–65.

NEAVE, F. 1949. The spread of the Japanese little-neck clam in British Columbia waters. *Fish. Res. Bd. Canada, Pacific Prog. Rept.*, No. 61, p. 13.

NELSON, T. C., AND E. B. PERKINS. 1931. Annual Report of the Department of Biology for the year ending June 30, 1930. New Jersey Agr. Exp. Sta.

NEWCOMB, W. 1875. Description of a new species of shell from San Francisco Bay. *Proc. California Acad. Sci.*, **5**: p. 415.

NEWCOMBE, C. F. 1893. Report on the marine shells of British Columbia. Bulletin of the Natural History Society of British Columbia, 1893, 31 pp.

ORTON, J. H. 1937. Some interrelations between bivalve spatfalls, hydrography and fisheries. *Nature*, **140**(3542): 505.

PACIFIC OCEANOGRAPHIC GROUP. MS, 1954. Physical and chemical data record — Strait of Georgia, 1949–1953. Joint Committee on Oceanography, 437 pp.

MS, 1963. Observations of sea water temperature, salinity, and density on the Pacific Coast of Canada. Fish. Res. Bd. Canada and Joint Committee on Oceanography, Vol. 1–23.

PICKARD, G. L. 1953. Oceanography of British Columbia mainland inlets. II. Currents. *Fish. Res. Bd. Canada, Pacific Prog. Rept.*, No. 97, pp. 12–13.

PRITCHARD, D. W. 1953. Distribution of oyster larvae in relation to hydrographic conditions. Proceedings of the Gulf and Caribbean Fisheries Institute, 5th Session, 1952, pp. 123–132.

QUAYLE, D. B. 1952. Structure and biology of the larva and spat of *Venerupis pullastra* (Montagu). *Trans. Roy. Soc. Edinburgh*, **62**(1)(8): 255–297.

MS, 1954a. Oyster Bulletin. British Columbia Department of Fisheries. Shellfish Laboratory, Ladysmith, B.C., **5**(1): 1–21.

MS, 1954b. Oyster Bulletin. *Ibid.*, **5**(9): 1–14.

MS, 1956. Oyster Bulletin. *Ibid.*, **7**(1): 1–16.

MS, 1957. Oyster Bulletin. *Ibid.*, **8**(2): 1–32.

1959. The early development of *Bankia setacea* Tryon, pp. 157–171. *In* D. L. Ray, [ed.] Marine boring and fouling organisms. Univ. Washington Press, 536 pp.

RICKETTS, E. F., AND J. CALVIN. 1952. Between Pacific Tides, 3rd ed. Stanford Univ. Press, 502 pp.

SCHELTEMA, R. S. 1962. Environmental factors affecting length of pelagic larval development in the gastropod, *Nassarius obsoletus*. *Amer. Zoologist*, **2**(3): 15.

SMITH, H. M. 1896. A review of the history and results of the attempts to acclimatize fish and other water animals in the Pacific States. *Bull. U.S. Fish. Comm.* for 1895, pp. 379–472.

SMITH, J. E. 1953. The maintenance and spread of sea-shore faunas. Sectional address, *Brit. Assoc. Adv. Sci.*, **10**(38): 145–156.

STAFFORD, J. 1914–18. The native oyster of British Columbia (*Ostrea lurida* Carpenter). *Rept. Comm. Fish. British Columbia* for 1914, pp. 140–160; 1915, pp. 100–117; 1916, pp. 79–101; 1917, pp. S88–S116; 1918, pp. Q91–Q112.

STEARNS, R. E. C. 1881. *Mya arenaria* in San Francisco Bay. *American Naturalist*, Vol. 15.

TAYLOR, G. W. 1895. Preliminary catalogue of the marine Mollusca of the Pacific Coast of Canada, with notes on their distribution. *Trans. Roy. Soc. Canada*, Ser. 2, Sec. IV **1**: 17–100.

THOMPSON, W. F. 1914. Report on the clam beds of British Columbia. *Report of the Commissioner of Fisheries, British Columbia*, for 1913, pp. R103–R125.

THOMPSON, W. F., AND R. VAN CLEVE. 1936. Life history of the Pacific halibut. (2) Distribution and early life history. *Rep. Internat. Fish. Comm.*, No. 9, 184 pp., Seattle.

THORSON, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, **25**(1): 1–45.

1946. Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Danm. Fiskeri- og Havunders., Ser. Plankton*, **4**(1): 1–523.

1957. Bottom communities (sublittoral or shallow shelf). *In* Geol. Soc. America, Memoir 67, **1**: 461–534.

TRITES, R. W. 1956. The oceanography of Chatham Sound, British Columbia. *J. Fish. Res. Bd. Canada*, **13**(3): 385–434.

TULLY, J. P. 1937. Oceanography of Nootka Sound. *J. Biol. Bd. Canada*, **3**(1): 43–69.

1949. Oceanography and prediction of pulp mill pollution in Alberni Inlet. *Bull. Fish. Res. Bd. Canada*, No. 83, 169 pp.

TULLY, J. P., AND A. J. DODIMEAD. 1957. Properties of the water in the Strait of Georgia, British Columbia, and influencing factors. *J. Fish. Res. Bd. Canada*, **14**(3): 241–319.

TURNER, H. J. 1953. A review of the biology of some commercial molluscs of the east coast of North America. 6th Rept. Invest. Shellfish. Mass., Dept. Nat. Res. Div. Mar. Fish. Commonwealth of Massachusetts, pp. 39–74.

WALDICHUK, M. 1957. Physical oceanography of the Strait of Georgia, British Columbia. *J. Fish. Res. Bd. Canada*, **14**(3): 321–486.

1958. Drift bottle observations in the Strait of Georgia. *Ibid.*, **15**(5): 1065–1102.

WALDICHUK, M., AND S. TABATA. 1955. Oceanography of the Strait of Georgia. V. Surface currents. *Fish. Res. Bd. Canada, Pacific Prog. Rept.*, No. 109, pp. 30–33.

WILSON, D. P. 1937. The influence of the substratum on the metamorphosis of *Notomastus* larvae. *J. Mar. Biol. Assoc. U.K.*, **22**: 227–243.

1951. Larval metamorphosis and the substratum. *Ann. Biol.*, **27**(7): 259–269.

1958. Some problems in larval ecology related to the localized distribution of bottom animals, pp. 87–103. *In* A. A. Buzzati-Traverso, [ed.] Perspectives in marine biology. Univ. of California Press.

YASUDA, J. 1952. Tidal and diurnal changes of occurrence of molluscan larvae at Maeshida Aichi Prefecture. *Bull. Jap. Soc. Sci. Fish.*, **17**(11): 342–344.

ZOBELL, C. E., AND E. C. ALLEN. 1935. The significance of marine bacteria in the fouling of submerged surfaces. *J. Bact.*, **29**: 239–251.

The Respiratory Metabolism and Swimming Performance of Young Sockeye Salmon[1,2]

By J. R. Brett

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

The rate of oxygen consumption in young sockeye salmon (*Oncorhynchus nerka*) was determined for various swimming speeds, including fatigue levels, at temperatures of 5, 10, 15, 20, and 24°C. A logarithmic increase in oxygen demand with increase in swimming speed characterized each acclimation temperature. Extrapolation to zero activity (standard metabolism) and maximum activity (active metabolism) provided differences of the order of 10 to 12 times the minimum rate.

The greatest scope for activity occurred at 15°C with an average active metabolic rate of 895 mg O_2/kg/hr for a swimming speed of 4.1 body lengths per second, just maintained for 1 hr. Above 15°C active metabolism was limited, apparently by oxygen availability.

Rate of replacement of oxygen debt following fatigue was determined by tracing the return to a resting state of metabolism, and confirmed by re-tests at fatigue velocities. In most instances the rate declined logarithmically with time; in some there was an initial or secondary slump. Times to recovery (return of spontaneous activity) averaged 3.2 hr, independent of acclimation temperature.

Swimming speed–fatigue tests indicated a sustained level of performance at about 200–300 min. Comparison with other fish suggests a marked change in slope of the fatigue curve at about 20 sec. The effect of temperature was greatest on sustained speeds and least on burst speeds.

CONTENTS

	Page
Introduction	1184
Materials and Methods	1185
Respirometer	1185
Fish chamber	1187
Fish culturing and preparation	1188
Experimental procedure	1188
Swimming speed	1190
Fish composition	1190
Results and Observations	1191
Preliminary tests	1191
Metabolic rates	1193
Oxygen debt	1196
Swimming speed and fatigue time	1197

[1]Received for publication June 2, 1964.

[2]Paper No. 11 concerning the physiology and behaviour of salmonid fishes, from the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

PAGE

DISCUSSION 1202
Validity of metabolic rate – swimming speed relation 1202
Metabolic rates, temperature, and activity relations 1203
Metabolic scope 1207
Weight relations 1209
Condition factor 1211
Fish composition 1212
Oxygen debt 1213
Swimming speed 1216
GENERALIZED RELATIONS 1220
SUMMARY AND CONCLUSIONS 1222
ACKNOWLEDGMENTS 1224
REFERENCES 1224
APPENDIX 1226

INTRODUCTION

ALTHOUGH MANY STUDIES have been made on the respiratory metabolism of fish (Winberg, 1956; Fry, 1957) none has been concerned with the exact requirements for swimming at various levels of sustained capacity. The majority of studies have aimed at obtaining either the minimum resting rate (standard) or maximum sustained rate (active) while considering the consequences of altering one or more environmental variables such as temperature (Job, 1955), oxygen and carbon dioxide concentrations (Basu, 1959), salinity (Hickman, 1959), and photoperiod (Evans *et al.*, 1962).

Since fish are neither continuously resting nor persistently active there has been a need to determine the metabolic cost for intermediate levels of some well-defined activity (Brett, 1962). Because of this need and the particular concern over the energy requirements for migration in salmon (Idler and Clemens, 1959), a detailed study of the respiratory metabolism and swimming capacity of yearling sockeye was undertaken.

It was first necessary to develop a respirometer which would impose precise water velocities on the fish, minimizing any advantage from wall effect or irregular flow patterns. In addition ample space for free swimming was desirable without sacrificing sensitivity to oxygen change by involving too large a volume of circulating water. By determining the rate of oxygen consumption over a series of increasing velocity steps it was expected that the necessary parameters of metabolism in relation to swimming speed would be obtained.

Beyond meeting the hydrodynamic requirements, there were other essential problems to be solved. These included stimulating the fish to swim without inducing excessive excitement or unnecessary energy dissipation, accounting for the possible involvement of oxygen debt, and ensuring that the fish performed maximally without injury.

Various units of measurement, either in the foot-pound or metric system, occur throughout the text. In order to avoid re-expression of one in terms of the other in every instance, a conversion table appears as an Appendix. Where suitable, both systems have been included in the figures. Unless otherwise stated, statistical limits are given as ± one standard error.

MATERIALS AND METHODS

RESPIROMETER

The respirometer was designed as a recirculating water tunnel incorporating an acrylic plastic fish-chamber (4½-inch inside diameter × 12 inches long) connected to a pump through fibreglass contraction and expansion cones (Fig. 1 and 2; Mar, 1959). The drive unit (3 hp electric motor, top-mounted on a variable-speed hydraulic gear) and centrifugal pump were separately mounted from the tunnel section, and connected to it through rubber expansion joints to reduce vibration transfer. Maximum output was 235 gal/min against a developed head of 40 ft, providing a maximum velocity of 3.7 ft/sec through the chamber. Total volume of circulated water was 7.32 gal.

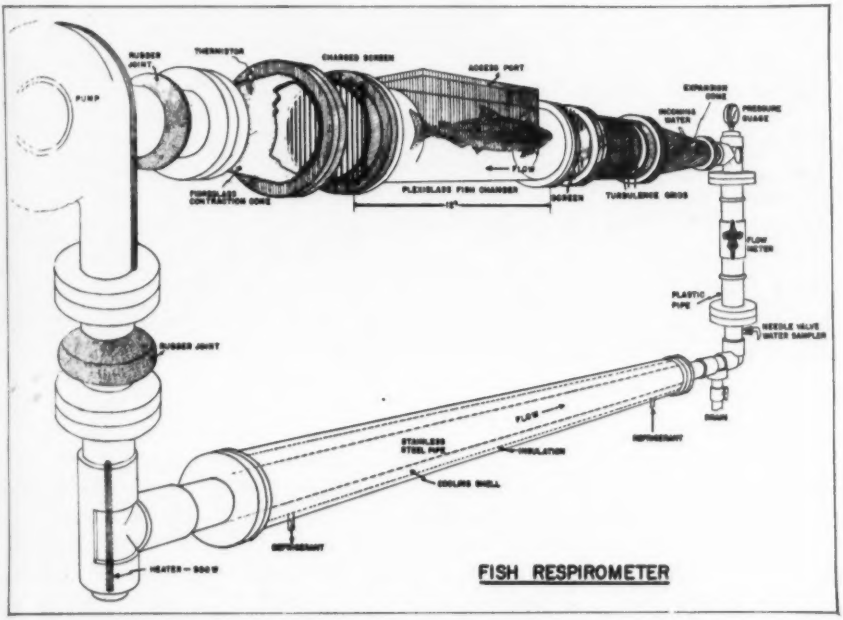


FIG. 1. Semidiagrammatic drawing of respirometer, expanded to show charged screen and turbulence grids.

A relatively consistent, flat velocity profile occurred over the range of velocities at which fish were forced to swim (0.3–3.3 ft/sec). This was achieved by the use of an appropriately designed diffuser section (expansion cone) followed by a series of three turbulence grids (mesh opening = .0755 inch, approximately 2 mm) leading to the fish chamber. These served to eliminate any massive turbulence or eddies by producing a streamlined flow of minutely turbulent water. The pattern was observed by the use of threads and dyes, and by introducing supersaturated water which resulted in a fine stream of bubbles evenly dispersed downstream from the grids.

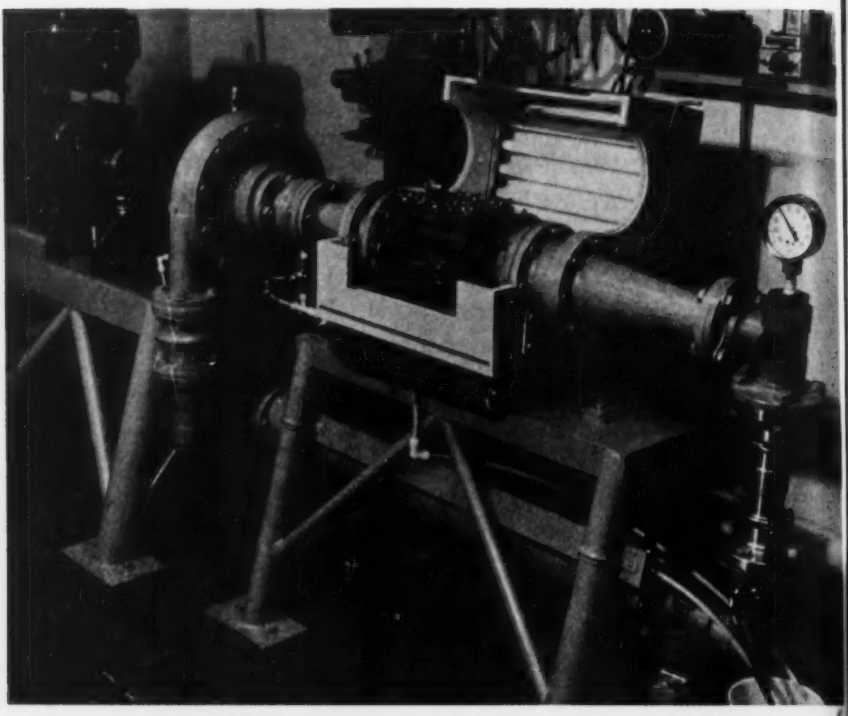


FIG. 2. Photograph of respirometer to show complete assembly.

The characteristics of the velocity profile in the chamber are important in the consideration of swimming speed. Laminar flow is not desirable since the velocity front is curved. Fine-meshed grids or honeycombs overcome this by producing a rectilinear front of statistically uniform turbulence. However, the turbulence has a characteristic rate of decay depending on the mesh size of the grids and water velocity. Eventually turbulent flow subsides to laminar flow. Calculations based on wind tunnel results (Goldstein, 1938) would indicate a probable decay from 2% to 0.7% turbulence over the length of the fish chamber. It would appear that sufficient turbulence persists to eliminate any advantageous wall effect developing at the downstream end of the chamber.

Temperature was controlled within ± 0.1°C by continuous flow of a refrigerant through a chilling jacket, counterbalanced by a 500-watt heater and relay. A turbine-type flow meter provided direct read-out of chamber velocity. Since the maximum cross-section of an average fish did not exceed 7% of the cross-section of the chamber, no adjustment for swimming speed error from this source was applied.

New water could be introduced to the system at any time from a reservoir located above the respirometer. Water from the reservoir was adjusted to be slightly higher in temperature and oxygen content than the circulating water.

By increasing the oxygen percentage under normal atmospheric pressure and causing slight cooling on introduction to the respirometer, supersaturation was avoided. The average oxygen content during the closed-circuit period approximated 100% of atmospheric oxygen (started at about 105% and respired down to 95%).

Fish Chamber

Movement of the fish was confined to the chamber by an array of vertical piano wires ($\frac{3}{8}$-inch spacing) imbedded in moulded fibreglass sections at either end of the chamber (Fig. 3). The downstream screen was electrified (60 cycle A.C.) through an isolated, variable transformer with an applied charge of 3–5 v. This was sufficient to cause definite avoidance without strong reaction. Fish quickly learned to occupy positions at least one or more inches upstream from the screen.

Voltage-controlled incandescent lighting from the top of a light-box provided good visibility. A forward cover area, darkened by a wide ring of black plastic, was provided and was frequently used by the fish. In addition, on the under side of the clear plastic chamber a dark rubber mesh was slung as a bottom reference plane. A wide access port, machined to fit exactly to the inside curvature of the tunnel, permitted ready loading with fish. By such means as these,

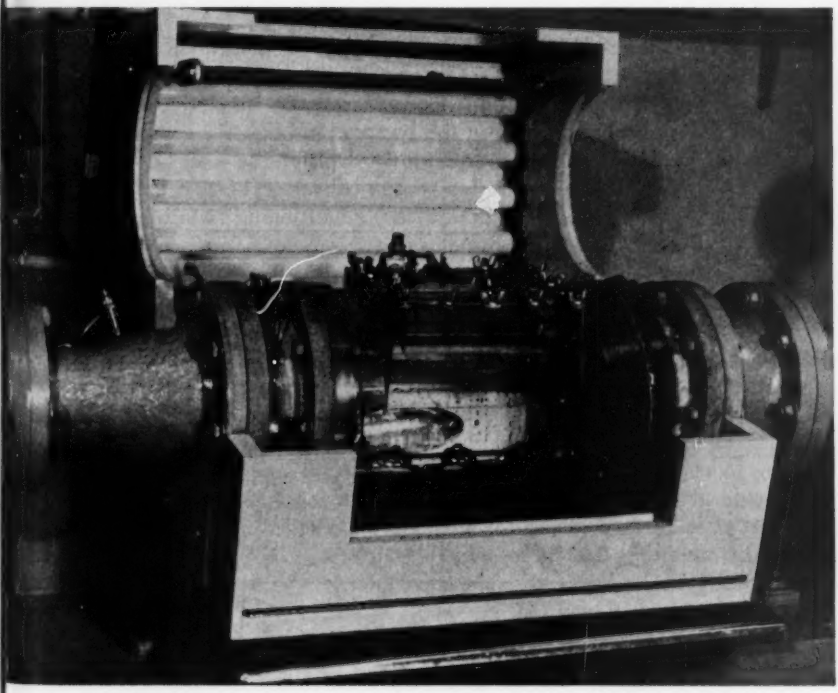


Fig. 3. Fish chamber with controlled light box open and one-way glass removed from viewing window.

an attempt was made to reduce excitement and promote good performance within the respirometer.

Fish Culturing and Preparation

Sockeye between 14 and 18 months of age were used (Table I). The fish were raised on a diet of Clark's pellet feed (J. R. Clark & Co., Salt Lake City, Utah) and a wet mix of canned salmon, pablum, cod liver oil, and yeast, bound with iodized salt. Pressure water-jets installed vertically in oval culture tanks produced an average velocity of about 0.7 ft/sec (range, 0.5–0.9) against which the fish swam constantly (Alderdice *et al.*, 1964).

Acclimation temperatures of 5, 10, 15, 20, and 24°C were maintained for at least 2 weeks within ±0.3°C of the desired final temperature. At temperatures above 10°C, intermediate steps of 5°C increments were maintained for 1 week. The 5°C fish were tested in April to coincide with the natural rise of environmental temperature above 4°C. All tanks were exposed to normal photo-period.

Test fish were not fed for a 24-hr period prior to being transferred in water to the respirometer. They were then set at a velocity of 0.3 ft/sec for an overnight conditioning period of 12–14 hr. Thus, a total of at least 36 hr fasting preceded any determinations of metabolic rate. An interval of this order has been shown by Beamish (1964a) to be necessary for determining the standard metabolism of brook trout. Where attempts were made to measure respiratory metabolism under resting conditions the water velocity was lowered to 0.1 ft/sec, which permitted the fish to rest on the bottom, and lighting reduced to 20 ft-c. In order to minimize vibration and sound transfer the usual drive unit was supplanted by a quiet $\frac{1}{3}$ hp Zero-Max torque converter, hooked up to the pump by a rubber V-belt. During the preliminary conditioning a continuous exchange of water was flushed through the respirometer.

Experimental Procedure

Following the introductory phase the fish were subjected to 75-min periods of swimming at fixed velocities. Commencing at 1.0 ft/sec the velocity was increased in steps of 0.3 ft/sec until the fish fatigued, usually after about 5–7 hr of performance, depending on size and condition. In each 75-min interval, exchange of water was cut off for the first 60 min; the last 15 min were used for flushing to re-establish the initial oxygen level. Three oxygen determinations were made at exactly 0, 30, and 60 min, each involving three samples. The first two were titrated, using the unmodified Winkler method. If the results differed by more than 0.02 ml sodium thiosulphate (0.1*N*), the third was titrated and the nearest two averaged. The repeatability was usually within ±0.01 ml thiosulphate (±0.016 ppm O_2).

Measurements of pH were taken before and after a test to obtain some indication of the effect of soluble excretory products. The initial readings averaged 6.8±.08 whereas those at fatigue time were 6.4±.11. The difference, most probably due to CO_2 and NH_3, was significant but not sufficient to cause

TABLE I. Metabolic rates and critical swimming speeds of yearling sockeye at five acclimation temperatures. The maximum and minimum observed oxygen consumptions are included together with the derived active and standard levels (by extrapolation).

Acclimation temperature	Total length	Wet weight	Condition factor	Maximum O_2-cons.	Minimum O_2-cons.	Active metabolism	Standard metabolism	Critical swimming speed	
	(*cm*)	(*g*)	(W/L^3)	(*mg/kg/hr*)	(*mg/kg/hr*)	(*mg/kg/hr*)	(*mg/kg/hr*)	(*ft/sec*)	(*L/sec*)
5°C									
Number	(9)	(9)	(9)	(9)	(9)	(9)	(9)	(9)	(9)
Mean	16.6	36.7	.769	537	66	514	41	1.76	3.26
S.D.	2.0	12.0	.076	...	...	94	9.7	...	.36
S.E.	0.7	4.0	.025	...	...	31	3.2	...	.12
10°C									
Number	(11)	(11)	(11)	(9)	(4)	(10)	(11)	(10)	(10)
Mean	16.2	32.9	.729	622	94	627	60	1.90	3.65
S.D.	2.3	13.1	.057	...	...	85	10.4	...	.30
S.E.	0.7	3.9	.017	...	...	27	3.2	...	.09
15°C									
Number	(10)	(10)	(10)	(8)	(7)	(8)	(10)	(8)	(8)
Mean	18.8	55.2	.786	988	121	895	71	2.52	4.12
S.D.	2.1	23.8	.098	...	...	123	11.4	...	.49
S.E.	0.8	9.5	.040	...	...	49	4.0	...	.19
20°C									
Number	(9)	(9)	(9)	(8)	(6)	(9)	(9)	(8)	(8)
Mean	19.5	62.6	.799	904	146	852	120	2.43	3.90
S.D.	3.0	24.6	.066	...	...	89	18.2	...	.40
S.E.	1.0	8.2	.022	...	...	30	6.1	...	.14
24°C									
Number	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
Mean	18.5	52.2	.822	882	259	848	196	2.25	3.75
S.D.	2.0	20.2	.090	...	...	87	29	...	.75
S.E.	0.9	9.0	.040	...	...	39	13	...	.34

concern (Brett, 1962). The high levels of metabolism obtained lend confirmation to this assumption.

Fatigue was considered present when the fish, by repeated efforts, could no longer hold itself off the electric screen. At this stage of near collapse the velocity was immediately lowered to 0.1 ft/sec, the electric charge turned off, and oxygen readings taken every 30 min to determine the rate of replacement of oxygen debt. Flushing was conducted only if the oxygen level fell below 70% air-saturation, in order to minimize disturbance yet not limit oxygen supply. In some instances after the rate of oxygen consumption had reached a minimum plateau and spontaneous movements had resumed, the same velocity as the final fatigue rate was re-imposed to test the recovery state. In others the "recovered" fish was returned to a culture tank and checked for condition on the following day.

Swimming Speed

The system of applying successive 75-min increments of increasing velocity resulted in the determination of a final swimming speed, maintained for some fraction of that time. In most instances fatigue occurred within 15–20 min of the start of the last imposed velocity. To allow for comparison on a uniform time basis it was decided to use 60-min sustained speeds as a standard, comparable with the time of steady performance set forth by Brett *et al.* (1958). Speed corrections for times less than 60 min were made on a proportional basis. Thus, if a fish having swum at 2.0 ft/sec successfully was required to swim at 2.3 ft/sec and fatigued in 20 min, its *critical swimming speed* was calculated as: $2.0 + (20/60 \times 0.3)$ ft/sec = 2.1 ft/sec. This arbitrary system was at least consistent, permitting comparison, and turned out to be surprisingly representative of threshold levels (see Results).

To answer the question of how the 60-min period related to longer or shorter intervals, a *fatigue time* vs *velocity* curve was determined by applying preset, fixed velocities and maintaining these until exhaustion set in. Two difficulties immediately arose, viz. how to ensure "resting fish" at the start, and how to eliminate interference from excited, erratic behaviour during a test. The method adopted was to accustom the fish for a number of weeks to swimming fairly rapidly in a large oval tank at approximately 1.0–1.2 ft/sec. They were then quickly transferred in water to the respirometer at the accustomed speed of 1.0 ft/sec for $\frac{1}{2}$ hr. The velocity was next raised to 2.0 ft/sec for 5 min to overcome extreme excitement from more rapid velocity increase (yet still within their capacity), then raised to the prescribed level. A maximum performance time was arbitrarily set at 1000 min (approximately 17 hr) for the first series, and subsequently lowered to 600 min (10 hr) for the second. One 4-day test was conducted.

Fish Composition

Since the metabolic rate for any organism is dependent on the total demand of all the tissues, it is desirable to know the composition of those tissues. A preponderance of stored fat, excessive body fluids, or heavy skeletal structure would reduce the proportion of "active tissues" and hence decrease the overall

rate. Active metabolism might be expected to depend on the amount of protein, or more grossly the body nitrogen, provided the pool of non-protein nitrogen was not large. A 50-g sockeye is about 50% body musculature by weight.

Because of the relative ease of determinations, it was decided to compare the metabolic rate for wet weight, dry weight, and dry weight minus lipid, the latter being an approximation of the major protein fraction. Wet weight was determined immediately after an experiment by carefully removing external moisture with absorbent paper. The fish was then frozen at −10°C, and subsequently ground to a fine homogenate. A weighed fraction (approximately ⅓) was oven-dried at 100°C for 18 hr. The balance was further ground with addition of distilled water to the original moisture level. Lipid determinations were then made in triplicate, following the method of Folch *et al.* (1957). No evaluation was made of the possible small lipid loss from different times of cold storage (up to 8 months).

RESULTS AND OBSERVATIONS

Preliminary Tests

In order to establish the nature of the relation between oxygen consumption and swimming speed, preliminary experiments with repeated measurements at the same velocity were conducted, including a prolonged series at 0.1 ft/sec.

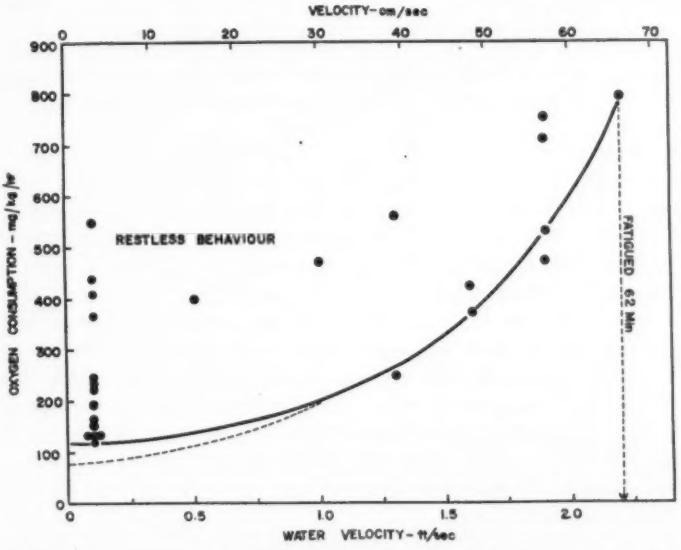


FIG. 4. Oxygen consumption and activity of a 16.5-cm, 30.3-g sockeye at 10°C. Repeated observations over 24 hr are shown at a near-resting velocity of 0.1 ft/sec. Other repeated measurements at higher velocities indicate the elevated rates which occur due to excitement, frequently accompanied by fluttering. The solid line represents the provisional relation; the broken line is the shape for a true exponential curve.

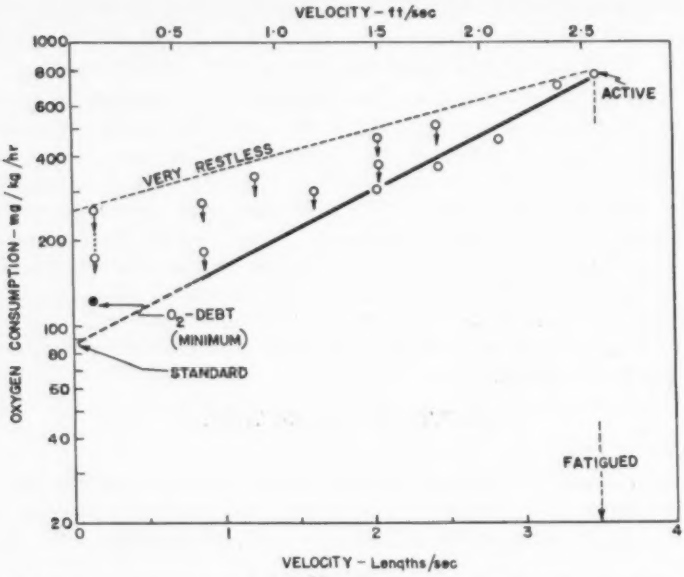


FIG. 5. Oxygen consumption and activity of a 22.4-cm, 83.8-g sockeye at 20°C. Arrow indicates that a lower value would be expected because of observed restless behaviour at the indicated velocity. Broken heavy line is extrapolated below minimum value obtained during recovery from oxygen debt.

The results of such an experiment are plotted in Fig. 4 and transformed in Fig. 5 to the logarithm of oxygen consumption in relation to velocity in terms of fish lengths per second (L/sec). The latter unit (ratio of speed to total lengths of fish) allows for comparison of fish of different lengths, and has been shown by Bainbridge (1958) to be a useful basis for more general comparisons. It was apparent that excitement or restlessness (spontaneous activity) could elevate the metabolism at low velocities to that accompanying much higher velocities. The reverse, in the form of lowered respiration at high velocities, was not observed although slight variations below a line drawn through the lowest points did occur. These were considered to be either experimental error or cases where partial oxygen debt had accumulated with the result that the measured rate of oxygen consumption was less than the actual energy required. There appeared to be a lower plateau of metabolism below which young sockeye would not readily reduce their level of excitement.

In a few cases the last metabolic rate preceding fatigue showed a slump below the previous reading obtained at a lower velocity. The reason is not known; it may relate to partial cardiac failure. In such cases the active metabolic rate was determined by extrapolation to the maximum 60-min sustained speed. Still others showed an increase above expected values, apparently related to bursts of swimming against the forward screen. This accounts for the difference

in Table I between the maximum observed oxygen consumption and the estimated active metabolism.

Metabolic Rates

The results for an average of ten sockeye at each of the various acclimations from 5°C to 20°C are presented in Table I. Difficulty in holding stocks at 24°C and in obtaining satisfactory behaviour in the respirometer at this near-lethal level reduced the number of completed runs to five.

For any one acclimation temperature fish can vary in the position, slope, and terminal point (fatigue level) of their metabolic rate in relation to swimming speed (Fig. 6). These differences may result from variation in composition, or in body form for the same weight or length (affecting drag and speed in terms of length/sec), or from differences in physical condition related to previous exercise (Brett *et al.*, 1958; Hochachka, 1961). If the mean is plotted for each acclimation, a series of lines in the form depicted in Fig. 7 is obtained showing the increase in metabolism with temperature in relation to swimming speed (Table II).

Standard metabolism rose from 41±3.2 mg O_2/kg/hr at 5°C to 196±13 mg O_2/kg/hr at 24°C. The active metabolic rates for the corresponding temperatures

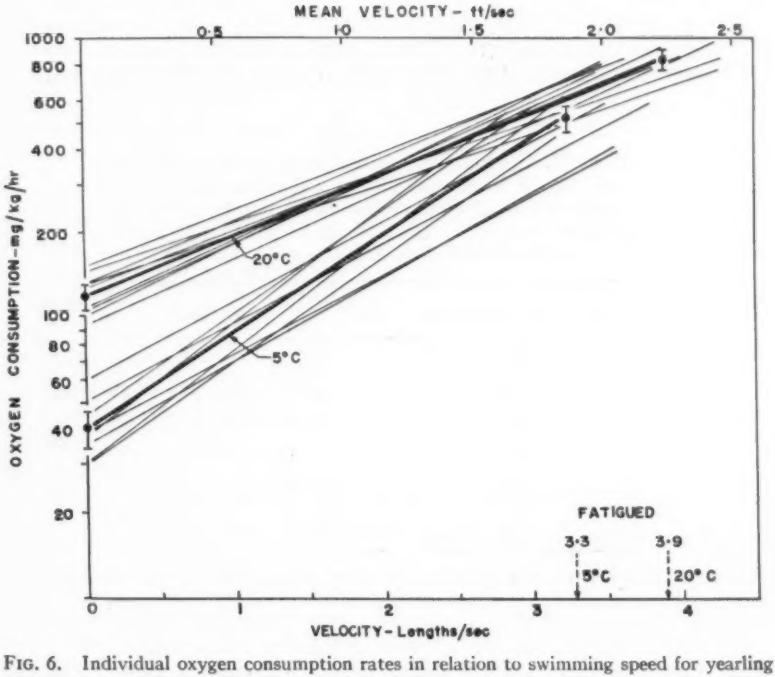


Fig. 6. Individual oxygen consumption rates in relation to swimming speed for yearling sockeye (average 18 cm, 50 g) at two acclimation temperatures (light lines). Mean lines of best fit are shown joining the mean ±2 S.E. of the standard and active metabolic rates (heavy lines).

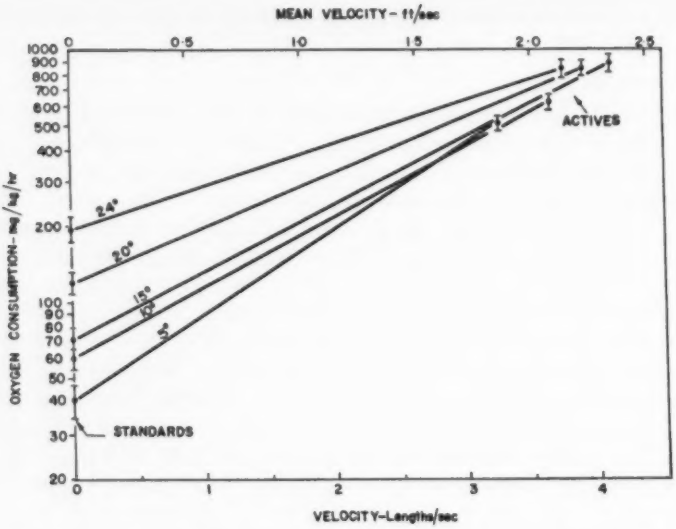


FIG. 7. Mean ±2 S.E. oxygen consumption rates in relation to swimming speed of young sockeye (18 cm, 50 g) for five acclimation temperatures. The crossing over the 5 and 10°C lines is within the expected limits of variability.

TABLE II. Equations for: A. relation of rate of oxygen consumption (Y in mg O_2/kg/hr) to swimming speed (X in Length/sec) at different acclimation temperatures, and B. relation for rate of oxygen replacement (Y in mg O_2/kg/hr) following fatigue (X in hours) (see Fig. 7 and 10).

Acclimation temperature		Equation
	°C	
A.	5	$\text{Log } Y = 1.61 + 0.34\ X$
	10	$\text{Log } Y = 1.78 + 0.28\ X$
	15	$\text{Log } Y = 1.85 + 0.27\ X$
	20	$\text{Log } Y = 2.08 + 0.22\ X$
	24	$\text{Log } Y = 2.29 + 0.17\ X$
B.	5	$\text{Log } Y = 2.40 - 0.16\ X$
	10	$\text{Log } Y = 2.55 - 0.18\ X$
	15	$\text{Log } Y = 2.64 - 0.15\ X$
	20	$\text{Log } Y = 2.65 - 0.12\ X$
	24	$\text{Log } Y = 2.66 - 0.06\ X$

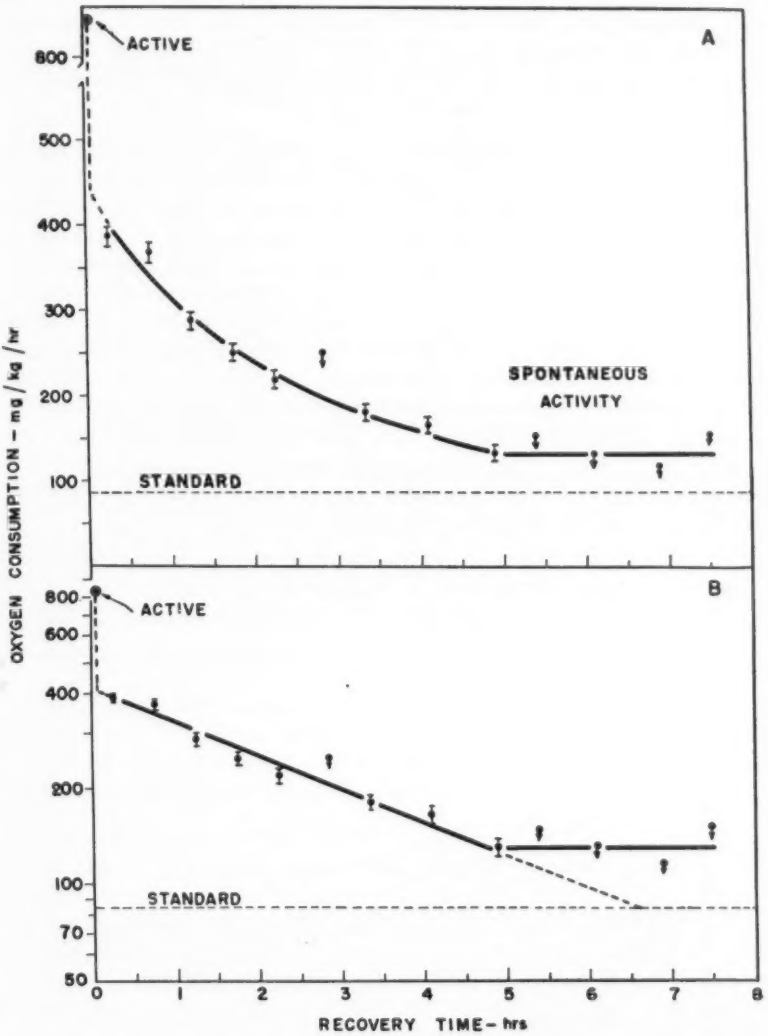


FIG. 8. Oxygen debt replacement in a yearling sockeye (21.5 cm, 87.9 g, 15°C) at rest following fatigue. Last recorded metabolic rate when swimming indicated by Active rate. Arithmetic plot in A transformed to semi-log relation in B. Extrapolation to zero time gives maximum non-swimming rate of oxygen consumption; extrapolation to standard rate gives expected time to complete recovery. Limits are shown equivalent to ±.04 ppm, involving two values (subtracted). Arrows as in Fig. 5.

were 514±31 and 848±39 mg O_2/kg/hr. Maximum active metabolism occurred at 15°C with a rate of 895±49 mg O_2/kg/hr. Although the latter is not significantly different from either the 20°C or the 24°C rate ($P \approx 0.5$ in both cases, by "t" test) the decreasing trend at higher temperatures suggests that oxygen availability was limiting, and that the differences were real (see Discussion).

Oxygen Debt

Following fatigue (with water velocity reduced) the exhausted fish would lie quietly in the forward part of the chamber, respiring deeply. Not infrequently the caudal fin would arch upwards almost in reflex reaction to more extreme ventilation gasps. In many instances this behaviour would persist for 2–4 hr, interspersed with an odd restless movement or exploratory turn. Spontaneous activity of a more continuous nature followed, elevating or affecting metabolism in such a way that the further replacement of oxygen debt could not be distinguished. The rate of decrease in oxygen consumption during the recovery period was discovered to be exponential (Fig. 8 and 18). Exceptions occurred in 29% of cases (n = 38) in which either a primary or secondary slump in metabolic rate occurred, followed by a return to a normal pattern of decrease. Frequently the lowest oxygen consumption recorded during recovery was lower than any obtained while trying to determine standard metabolism directly, yet not quite as low as the extrapolated estimate (see Fig. 5).

Having obtained a suitable linear transformation it was possible to treat the data on recovery rate much as those for swimming requirements. An eyed line-of-best-fit was drawn for each applicable case, and the mean value determined

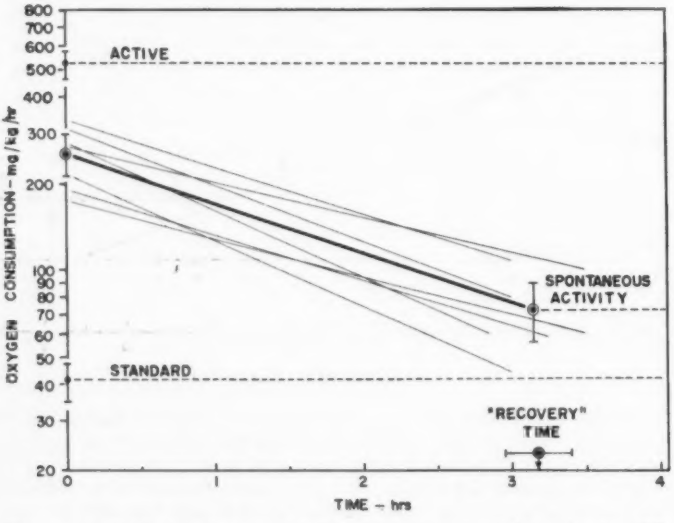


FIG. 9. Individual and mean ±2 S.E. oxygen consumption rates for 5°C-acclimated yearling sockeye during replacement of oxygen debt. Mean time ±2 S.E. to start of spontaneous activity shown.

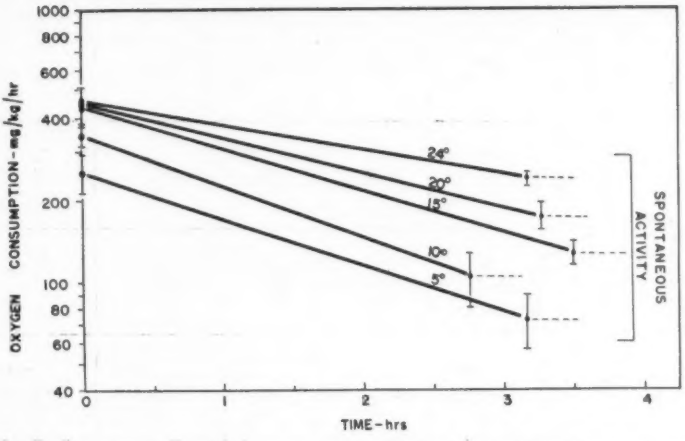


FIG. 10. Mean ±2 S.E. oxygen consumption rates during replacement of oxygen debt in yearling sockeye at five acclimation temperatures.

for initial metabolic rate, final rate (before start of spontaneous activity), and the time to this stage of recovery (Fig. 9 and 10). The areas under each curve for each acclimation were then computed to provide a measure of the total sustained debt as mg O_2/kg (Table III).

No deaths occurred in the recovery phase for acclimations up to 15°C. In the cases examined for a number of days after fatigue, normal feeding had commenced on the following morning (about 18 hr later).

At 20°C, greater irregularity in recovery rate occurred with some loss of equilibrium; one out of nine fish died. Increased problems of recovery were apparent in the 24°C group where, as stated, only five fish out of an original ten could be tested successfully. Of these five, two were highly irregular in metabolic rate but recovered, and two died (see Fig. 19).

SWIMMING SPEED AND FATIGUE TIME

The first series of tests to determine a velocity–fatigue curve were performed from June 11 to 15, 1962, on 17 yearling sockeye (Table IV). Difficulty in obtaining a mean fatigue time for a given velocity resulted from the great range of fatigue times at intermediate velocities, which suggested poor response in some fish. In addition, assigning a fatigue time for those fish still swimming at the end of the test period posed a problem.

A second series was conducted from February 11 to 14, 1963, using 35 fish to supplement the data for the first group (Table V). Although at the same acclimation temperature and approximately the same size, these fish had a reduced capacity to perform.

Similar experiments, conducted with larger numbers of adult salmon during the following spring showed normal distribution of fatigue times when the proportion of a sample showing fatigue was plotted as probits against the logarithm of time-to-fatigue. This system of plotting is essentially the approach of

TABLE III. Metabolic rate, recovery time and magnitude of oxygen debt following fatigue of yearling sockeye at five acclimation temperatures. The maximum rates were obtained by extrapolation (see Fig. 8) For comparison the observed rates in the first ½-hr are shown. Column 5 shows the ratio of maximum recovery rate (non-swimming) to the active metabolic rate. Two recovery times are given, one as the time observed to the start of spontaneous activity and the other as the time determined by extrapolation to reach standard metabolism (Fig. 8). The former provides an "overload" oxygen debt and the latter a calculated total debt.

Acclimation temperature	Maximum rate	Rate in 1st ½-hr	Recovered rate	Max. rate of activity	Recovery time	Average test time	Deaths	Oxygen-debt		Time to "full recovery"	Successful retests
								Overload	Total		
	(*mg/kg/hr*)	(*mg/kg/hr*)	(*mg/kg/hr*)	(%)	(*min*)	(*min*)	(%)	(*mg/kg*)	(*mg/kg*)	(*min*)	(*no*)
5°C											
Number	(7)	(6)	(7)		(7)	(7)	(7)	(7)	(7)	(7)	(2)
Mean	253	212	73	49	190	244	0	252	350	278	2
S.D.	56	...	22		19			51.4			
S.E.	21	...	8.3		7.2			19.5			
10°C											
Number	(7)	(7)	(7)		(6)	(7)	(7)	(6)	(6)	(6)	(1)
Mean	343	308	105	55	167	243	0	292	457	245	0
S.D.	41	...	32		39			18.7			
S.E.	15	...	12		16			7.1			
15°C											
Number	(8)	(8)	(8)		(8)	(8)	(8)	(8)	(8)	(8)	(2)
Mean	439	384	128	49	211	297	0	504	680	315	2
S.D.	68	...	18		79			18.2			
S.E.	24	...	6.7		28			6.4			
20°C											
Number	(6)	(6)	(6)		(7)	(7)	(9)	(6)	(6)	(6)	(3)
Mean	448	392	175	50	196	288	11	450	585	274	3
S.D.	72	...	28		69			21.2			
S.E.	29	...	11		26			8.6			
24°C											
Number	(4)	(4)	(4)		(2)	(4)	(5)	(3)			
Mean	461	421	243	54	190[a]	300	40	287	...[a]	...[a]	
S.D.	33	...	7		...			13.5			
S.E.	16	...	4		...			7.8			

[a]Since death occurred in 40% of this sample, no entry has been made.

TABLE IV. Fatigue times for 17 yearling sockeye (17.57±0.29 cm, 42.08±2.37 g) tested in June, acclimated to 10°C. Geometric mean times for grouped velocity intervals of ±0.2 L/sec are given. Limit of test time = 1000 min (17 hr); this has been the assigned "fatigue time" for fish still swimming at the end of a test.

	Velocity — (*L/sec*)						
	3.7	3.9	4.1	4.3	4.5	4.7	4.9
Fatigue time (*min*)	1000 1000	1000	1000 5.8 11.6 1000	2.7 4.9 20.3 93.0	5.0	2.3 3.3 5.3	2.7 6.8
G.M. ±S. E.	1000	50.7 (174 / 15)		10.5 (20 / 5.5)		3.7 (6.5 / 2.1)	
Grouped velocity range	3.7±.1	4.0±.2		4.4±.2		4.8±.2	

TABLE V. Fatigue times for 35 yearling sockeye (18.61±.14 cm, 52.82±3.76 g) tested in February, acclimated to 10°C. Geometric mean times and time-to-50%-fatigue from Fig. 11 are given. Limit of test time = 600 min (10 hr).

	Velocity — (*L/sec*)								
	2.6	2.8	3.0	3.2	3.4	3.6	3.8	4.0	4.4
Fatigue time (*min*)	600 600 600	600	55 600 600	9.3 15 75 335	3.7 315 600	1.5 2.2 5.7 9.5 31 40 100	1.0 1.5 2.0 26.3 35 600[a]	2.0 3.3 5.3 6.1 9.0 20.0	0.1 0.6
G.M. ±S. E.	600+		94.9 (182 / 50.1)		20.8 (39.8 / 11.0)		5.3 (7.8 / 3.7)		0.25
FT_{50}	600+		112		13.2		4.7		....
Grouped velocity range	2.7±.2		3.1±.2		3.5±.2		3.9±.2		4.4

[a]Not included in G.M. Considered exceptional from probit plot, Fig. 12.

[a]Since death occurred in 40% of this sample, no entry has been made.

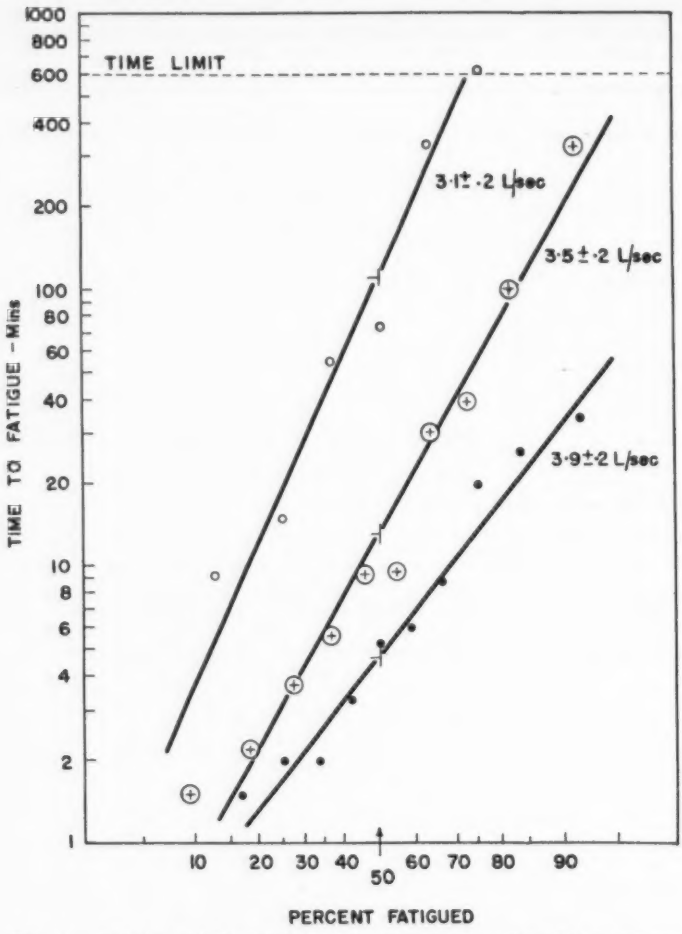


FIG. 11. Relation of fatigue time (log) to order of fatigue (probit) for sockeye yearlings (18.6±0.14 cm, 52.8±3.8 g, 10°C) at three velocities (L/sec).

bio-assay analysis using fatigue time as the response and velocity as the dose. The method made it possible to obtain a *time-to-50%-fatigue* (FT_{50}), providing determinable, representative values where up to half the fish were still swimming at the end of the test period.

Although undesirably low in numbers of fish, the yearling sockeye data were treated in the above manner for the February series (Fig. 11), and both groups were analysed for geometric mean fatigue time to permit comparison (Fig. 12; Tables IV and V).

For the standard test time of 60 min used in the metabolism experiments the June sockeye had a maximum swimming speed of 4.0 L/sec whereas the

February rate was 3.2 L/sec. The geometric mean time-to-fatigue and the interpolated time-to-50%-fatigue approximated closely, substantiating the use of the latter for comparison where not all the fish fatigue in the allotted time. There is some suggestion in the data that the capacity to continue performing, once 200–300 min have elapsed, is greater than that expected by extrapolation. Of the four smaller fish subjected to long-term swimming, two fatigued within 180 min, whereas one continued for 5520 min (3.8 days at 4.8 L/sec, 15°C) and

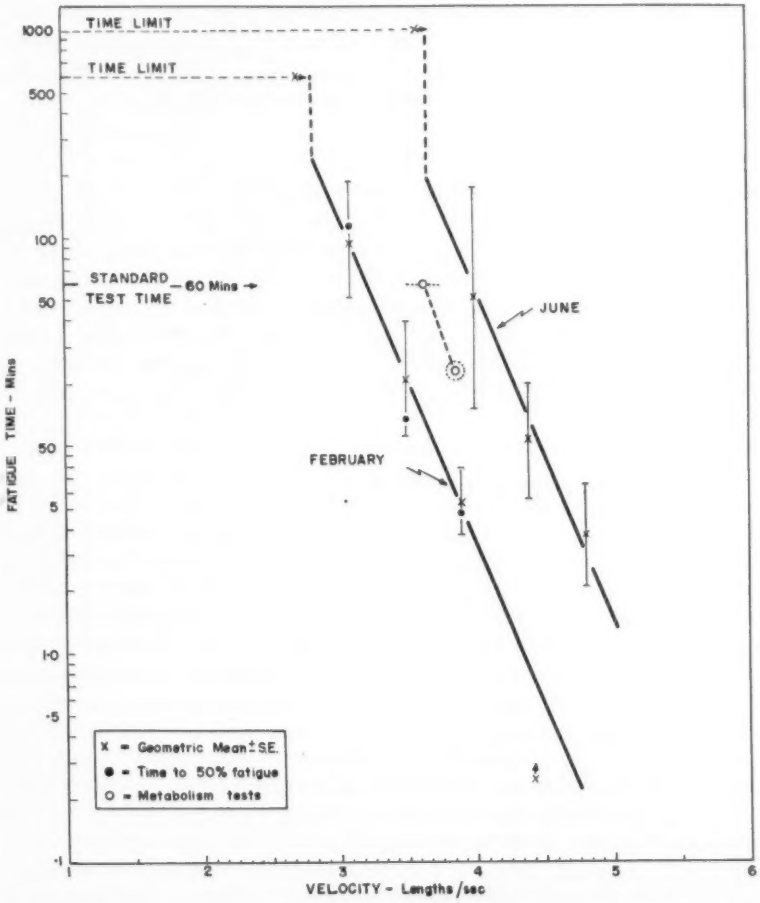


FIG. 12. Relation between geometric mean fatigue time and swimming speed for yearling sockeye at 10°C. June fish averaged 17.6 cm, 42 g, and February fish were 18.6 cm, 52.8 g. Time to 50% fatigue from probit plot (Fig. 11) falls within G.M. ±1 S.E. Mean fatigue time determined from metabolism tests is shown (circled) including 60-min calculated maximum speed. Point with arrow at bottom of graph involved only two excited fish. Points with arrows at top of graph indicate fish were still swimming at end of test time.

the fourth was still swimming at 5800 min (4+ days at 3.7 L/sec, equivalent to 92.3 miles). These latter performances demonstrate a remarkable sustained capacity beyond an apparent 200–300-min threshold level. For this reason dotted lines have been used in Fig. 12 suggesting a "break" in the fatigue curve.

The mean swimming speed and fatigue time in the metabolism studies using the step-type increase in velocity was 3.84 L/sec maintained for 23 min. Using the method described to determine a 60-min fatigue velocity, the result was 3.65 L/sec. These two values plotted in Fig. 12 are seen to parallel the fatigue curves, and by coincidence the value of 3.6 L/sec approximates the June threshold speed maintained for at least 1000 min. Hence it is quite likely that the values for "critical swimming speed" recorded in Table I approximate the threshold levels which would be obtained from fatigue curves.

DISCUSSION

Validity of Metabolic Rate–Swimming Speed Relation

Much of the essence of this study depends on the validity of the linearized relation between logarithm of oxygen consumption and swimming speed. The technique employed was expected to provide in a single test on individual fish both active and standard rates of metabolism, as well as maximum sustained swimming speeds. Since minimum and maximum activity levels would be obtained in a systematic way, it was further expected that the ultimate values for these extremes could be obtained within the limits of season and condition of the stocks tested.

The use of sensitive activity meters has served to show a direct (arithmetic) relation between the frequency of undefined, random movements and oxygen consumption (Spoor, 1946; Beamish and Mookherjii, 1964). This method has been employed mostly for determining standard metabolism by extrapolation to zero activity. Since the maximum observed metabolic rates are limited to those for spontaneous activity, estimates of active metabolism cannot be obtained. Fry and associates (Fry, 1957; Basu, 1959) used a rotating annular chamber, later modified into the form of a "doughnut", and induced fish to swim strongly by applying a localized electric field. Maximum rates of oxygen consumption were taken to be a good measure of active metabolism; however, no significant relation between speed of rotation and oxygen consumption was apparent (Basu, 1959). Saunders (1962) subsequently obtained considerably higher rates for two species at approximately the same calculated swimming speeds. The apparent lack of relationship between imposed velocity and metabolic rate in these cases was undoubtedly involved with excitement. Nevertheless, Fry (1957) was able to transform earlier data on a variety of species including four salmonids into an approximate linear relation between cruising speed and oxygen consumption, expressed as the square root of the difference between active and standard metabolism ($\sqrt{\text{"scope"}}$). Although the assumption that a full measure of active metabolism was obtained may not prove to be substantiated in every case, the derivation showed the possibility of an exponential relation between metabolism and swimming speed.

Wohlschlag (1957) and Wohlschlag and Juliano (1959) also used a rotating annular chamber, allowing the fish to swim "naturally" without particular persuasion from an applied stimulus. When corrected for weight and temperature, the logarithm of oxygen consumption was found to be directly related to velocity, although a fairly large standard error was involved. Hatanaka (personal communication) has approached the problem by studying the decrease in body weight in relation to swimming speed in a propeller-induced stream and found a linear relation between the logarithm of per cent decrease in body weight and velocity.

These related studies, conducted with somewhat less precision than that made possible in the present experiments, lend confirmation to the relation derived for the sockeye data[3]. It seems likely that the exponential transformation is one that applies to fish metabolism in general. However, the increase in drag on a non-flexing dead fish follows more standard hydrodynamic laws, where the log of "power to overcome drag" is directly related to the log of velocity, with appropriate constants (Brett, 1964). Blazka (1960) and Blazka *et al.* (1960) used a neatly devised respirometer with a small ratio of fish volume to water mass in which the fish almost brushed the walls of the respirometer chamber. They obtained a relation showing greater curvilinearity than that represented in Fig. 4. This may have arisen from proportionately increased drag due to acceleration of water past the body of the fish under the confined circumstances. The weight of evidence, however, supports the contention that the metabolic relation is best expressed in the form $Y = ae^{bX}$, where Y = oxygen consumption, X = swimming speed.

Metabolic Rates, Temperature, and Activity Relations

Accepting the validity of the relation plotted for the five acclimation temperatures in Fig. 7, it is possible to read off the metabolic rates accompanying intermediate velocities by interpolation and to construct the graph of Fig. 13. This shows the relation between given levels of activity and corresponding rates of oxygen consumption over the biokinetic range of the species.

Standard metabolism. The points for zero velocity, representing standard metabolism, are not significantly different between 10°C and 15°C ($P \approx .07$) although the means differ by 11 mg O_2/kg/hr. By graphic approximation (Fig. 14) it was determined that a line could be drawn to pass through the limits set by the mean ± 2 S.E. of each oxygen consumption rate with the equation:

$$\log (Y - 36) = 0.48 + 0.071\ X$$

where Y = oxygen consumption in mg O_2/kg/hr, and X = temperature in centigrade degrees.

This provided the most likely standard metabolic rate at each temperature and permitted extrapolation of the rates to the upper and lower lethal

[3]Observations on pumpkinseed (*Lepomis gibbosus*) also support the validity of this approach (Brett and Sutherland, MS, 1964).

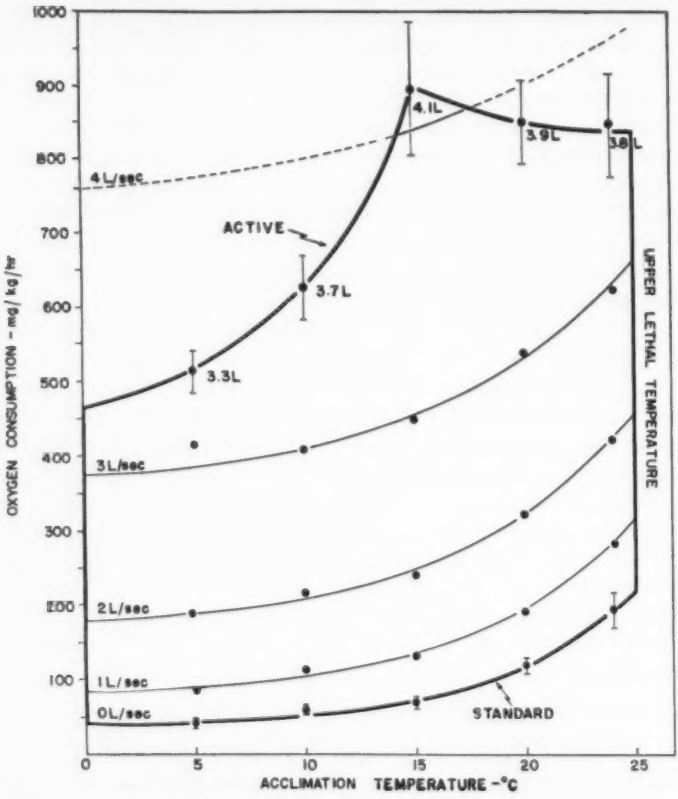


FIG. 13. Relation between oxygen consumption and temperature at various swimming speeds for yearling sockeye salmon (18 cm, 50 g). Standard and active rates are indicated as mean ±2 S.E. The 60-min "critical speed" accompanying each active rate is shown. Swimming speeds of 1–3 L/sec obtained by interpolation; those at 0 and 4 L/sec by extrapolation, except at 15°C. The broken line for 4 L/sec is drawn in an area where rapid fatigue would occur since the speed at these temperatures demands a metabolic rate in excess of the active rate.

temperatures of approximately 25°C and 0°C. The value of 36 mg O_2/kg/hr is considered to be the minimum threshold metabolism capable of supporting life of yearling sockeye at a low temperature. It is known that young sockeye can just survive freezing temperatures when acclimated to 5°C (Brett, 1952) and that young sockeye and chum salmon (*O. keta*) have an ultimate lower lethal of –0.1°C in 28‰ salt water (Brett and Alderdice, 1958). The extrapolated estimate for standard metabolism at 0°C was 39 mg O_2/kg/hr. Standard rates increased fairly rapidly above 15°C, with a calculated maximum of 220 mg O_2/kg/hr at 25°C.

These minimum and maximum levels of standard metabolism agree closely with what might be expected for brook trout (Beamish, 1964b). However, the concave relation of the sockeye data shows a somewhat lower rate at intermediate temperatures (Fig. 14).

ACTIVE METABOLISM. The sharp cut-off in active metabolic rate at 15°C (Fig. 13) suggested the presence of a limiting factor, suspected as being oxygen concentration. Although no significant difference was found between the maximum rates for 15, 20, and 24°C (page 1193) it is to be noted that the means do decrease. This circumstance was considered likely since the amount of oxygen per unit volume decreases with temperature (Fig. 15). To test this possibility, an experiment to determine the effect of relatively high levels of oxygen concentration (approximately 150% air-saturated) on active metabolism was performed at 20°C (Table VI). The initial results showed a highly signif-

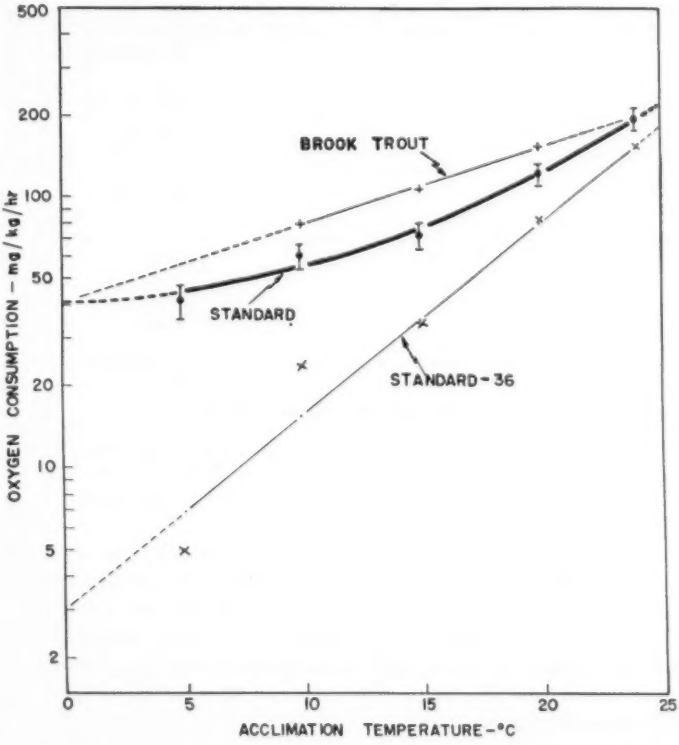


FIG. 14. Relation of standard metabolism to acclimation temperature for yearling sockeye (18 cm, 50 g). The line passing through the mean or within ±2 S.E. was obtained from the best straight line drawn through values of the *standard* –36. Standard rates for 100-g brook trout (Beamish, 1964b) are presented for comparison.

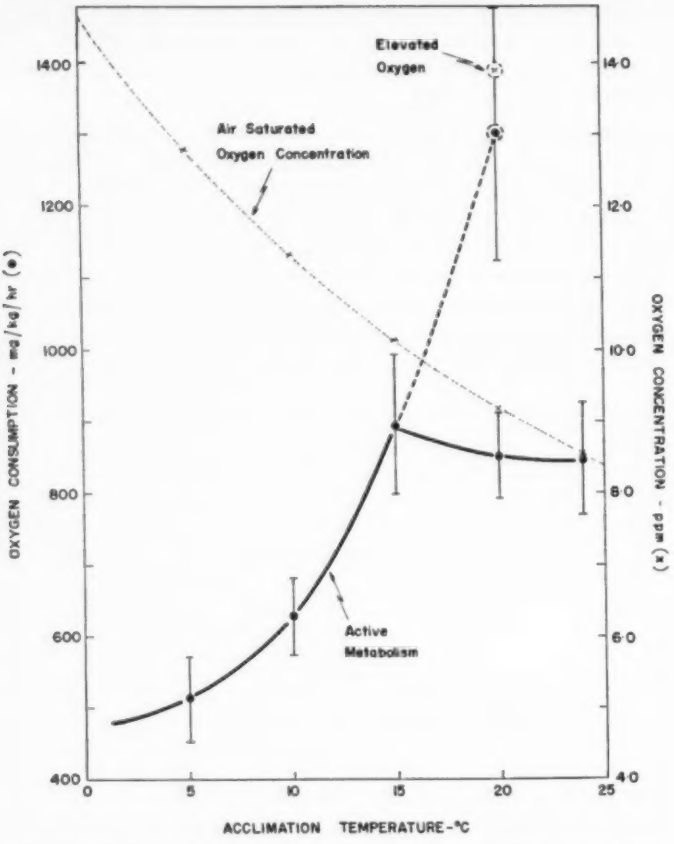


FIG. 15. Active metabolism of yearling sockeye (heavy line) tested at air-saturated oxygen levels (dotted line). Mean ±2 S.E. metabolic rate for elevated oxygen (13.9 ppm) determined at 20°C (circled points).

icant proportional increase in active metabolism which was elevated by an average of 50%. However, wide variation in the imposed oxygen levels occurred. A temporary halt was called in the tests in order to improve the controls. During this period the complete stock of yearling sockeye was accidentally lost. A new stock was obtained from a different source and found to be infected with a gill parasite (*Salmincola* sp.). The parasite was removed by cutting the hold-fast under anaesthetic.

A comparison of the new stock with the original stock revealed a lower active metabolic rate at 20°C, which was not quite significant ($P \approx .08$). In addition, elevated oxygen concentrations failed to bring about any significant increase in active metabolism (Table VI). Some slight "erosion" of gill lamellae had taken place as a result of the infection, but this did not appear to be sufficient

to produce such a marked difference in response between the two stocks. It was apparent that a thorough examination of the problem would be required before any satisfactory answer could be obtained.

The conclusion was that environmental oxygen concentration could be a limiting factor above 15°C, but that other factors of a physiological nature may occur to alter this relation.

The reason for fatigue at temperatures lower than 15°C must be sought beyond the respiratory circumstance in some incapacity to deliver available oxygen or maintain an adequate supply of metabolites. The maximum rate at 15°C of 895±45 mg O_2/kg/hr (Table I) is considerably higher than other maxima obtained for salmonids of about the same weight, e.g. 450 mg O_2/kg/hr for *Salvelinus fontinalis* (Job, 1955), and 460 mg O_2/kg/hr for *Salvelinus namaycush* (Gibson and Fry, 1954).

TABLE VI. Comparative rates of active metabolism for 20°C-acclimated yearling sockeye at various levels of oxygen concentration. Stock "A" is original stock from Great Central Lake; stock "B" is from Cultus Lake. See Table I for records on stock "A" at air-saturated levels of oxygen.

Stock	Active metabolism	Oxygen concentration		Critical speed	
	(*mg/kg/hr*)	(*ppm*)	(%)	(*ft/sec*)	(*L/sec*)
A					
Number	(6)	(6)	(6)	(5)	(5)
Mean	1302	13.9	152	2.39	4.27
S.D.	267	3.3	...	...	0.94
S.E.	89	1.3	...	...	0.43
B					
Number	(5)	(5)	(5)	(5)	(5)
Mean	740	8.71	95	1.94	2.98
S.D.	176	0.24	...	...	0.58
S.E.	80	0.11	...	...	0.26
B					
Number	(4)	(4)	(4)	(4)	(4)
Mean	755	13.02	142	1.98	2.84
S.D.	121	.50	...	...	0.28
S.E.	60	.25	...	...	0.14

METABOLIC SCOPE

One of the aims of this study was to determine the energy required solely for locomotion, at various levels of performance. By deducting the amount directed into maintenance (standard) the balance of oxygen consumption when swimming can be ascribed mostly to the mechanics of propulsion. This balance of "available energy" was termed the *scope for activity* by Fry (1957) when applied to the maximum metabolic difference at any one acclimation temperature (active minus standard). Beamish (1964b) has further introduced the term *routine scope* as the amount of metabolism devoted to spontaneous activity

(routine minus standard). A comparison of the power to overcome the drag on an average 50-g dead sockeye (freshly killed) and that expended by a 50-g living fish was made by Brett (1963) using metabolic scope determinations. The optimum relation in favour of the swimming fish occurred at about 4 L/sec. The metabolic scope for swimming at speeds of 1, 2, and 3 L/sec is depicted in Fig. 16. It is apparent that the respective requirements for standard metabolism and for swimming at 1 L/sec are approximately equal up to 12°C. A continuing rise in the maintenance fraction elevates the standard rate to almost that for 2 L/sec at 25°C. These relations serve to emphasize the dual increased costs imposed by temperature on metabolism. Not only does it cost more to swim at 1 L/sec with increasing temperature, but above about 12°C the maintenance fraction increases considerably.

Although slight but definite curvilinearity characterizes the distribution of points at low swimming speeds, a straight line has been used as a near approximation of the relation (maximum error = 6%). Using the general exponential equation (page 1203), the slopes for the speeds of 1, 2, and 3 L/sec are, respectively, .019, .013, and .007. The rate of decrease in slope is such that at 4.2

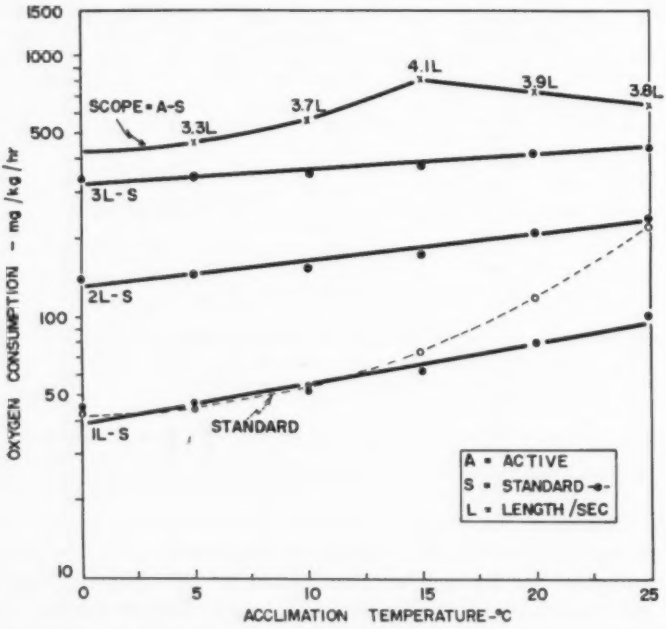


FIG. 16. Relation between metabolic scope (locomotor requirement) and acclimation temperature for various swimming speeds. The maximum scope with accompanying critical swimming speed is shown in the top line. The standard metabolic rate (*S*), the value subtracted in each case above, is included for comparison to show the "maintenance cost" at each temperature.

L/sec the slope would approximate zero. In other words, the temperature influence on locomotor metabolism is negligible at burst speeds (approximately 4–10 L/sec). As pointed out in a previous paper (Brett, 1964), it makes the thermal relations of metabolism for burst speeds comparable to those of a homeotherm. This important phenomenon was noted in a general way by Blaxter and Dickson (1959) while studying the burst speeds of a variety of marine species. The authors reported that "There was no consistent effect of temperature on the [burst][4] swimming speed over the range of temperature used", e.g. 5–18°C for herring.

Having established the relation for given swimming speeds, the further relation for the total scope (top line Fig. 16) can be seen to depend on the fact that increasing temperature permits a higher level of metabolic rate accompanied by a higher level of sustained performance. This increase is curtailed by available oxygen supply above 15°C, and performance and oxygen uptake both decline thereafter.

Weight Relations

A comparison of the weights between the sets of five acclimations showed that there were highly significant differences between the first group (5 and 10°C) and the second group (15 and 20°C), but not within these groups (Table VII). The 24°C-acclimated fish, with an intermediate mean weight, did not differ significantly from either of the other acclimation groups. The maximum difference in mean weight was that between 20°C and 10°C (62.6 g and 32.9 g, respectively).

As a result of this difference, a correction for weight would be necessary at each acclimation if there were a significant difference in rate of oxygen consumption with size (within the range considered), applied to standard and active rates.

Although there is abundant evidence for such corrections for standard metabolism, particularly the extensive series collected by Winberg (1956) at 20°C, nevertheless there are cases where the rates were almost directly proportional to weight (Wohlschlag and Juliano, 1959, July–Aug. equation; Hickman, 1959, winter starry flounder over 40 g; Beamish, 1964b, speckled trout, 10, 15, and 20°C). Comparable studies on active metabolism are scarce. Job (1955), investigating the active metabolism of speckled trout from 5 to 1000 g, demonstrated that at 5°C the exponent b equalled 0.94 indicating near proportionality, whereas at 20°C it was 0.75. Basu (1959) applied Job's b values to enable comparisons of active metabolism corrected for weight in speckled trout, and provided evidence for a value of 0.8 in carp at 30°C.

For the yearling sockeye data, over the range of weights studied, there was no significant correlation between weight and metabolic rate (mg O_2/kg/hr), either standard or active, for any of the acclimation temperatures. One series at 15°C acclimation did include a small group of underyearlings, introduced for weight comparison (Fig. 17). There was a correlation of –.45 for standard

[4]Durations of ½–1 min involved.

TABLE VII. Mean weight ±2 S.E. of yearling sockeye from each acclimation temperature. Significant difference between groups determined by "t" test (Goulden, 1952).

Mean weight (g)	±2 S.E.	Table of comparison between acclimation temperatures					
			5°C	10°C	15°C	20°C	24°C
36.70	± 8.0	5°C		N[a]	.10	.01[c]	N
32.85	± 7.8	10°C			.02[b]	.01[c]	.10
55.18	±19.0	15°C				N	N
62.58	±16.4	20°C					N
52.24	±18.0	24°C					

[a]N = not significant, by inspection.
[b]Significant.
[c]Highly significant.

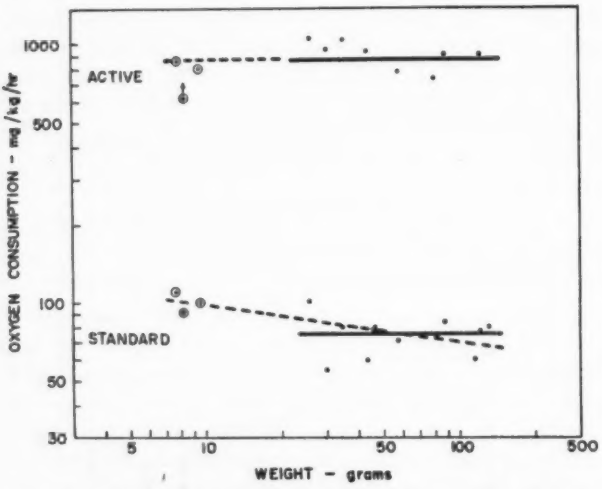


FIG. 17. Relation between weight and metabolic rate at 15°C for yearling sockeye (solid line) and that for a greater weight range including underyearlings (circled points). The latter were tested in groups of five fish; one series (with arrow) was not carried to maximum swimming speed.

rate and weight which was not quite significant ($P_{.05} = .53$)[5]. If a line of best fit is employed, however, the difference in standard metabolism at 32 g and 62 g is 7%. Since no such difference exists for active metabolism, this possible small error at the resting level was not sufficient to warrant further consideration.

[5]Alternatively it can be shown that the slope of the line relating log weight to log mg O_2/hr does not differ significantly from 1.0 (Table VIII).

The metabolism data can therefore be considered to apply to an overall mean weight of 47.9±2.3 g and length of 17.8±1.6 cm (n = 44), i.e. approximately 50 g and 18 cm.

Condition Factor

A condition factor or index relating weight to length (W/L^3) has frequently been used to provide a relative measure of well-being of fish (Carlander, 1950). This is a different concept from condition in terms of physical fitness, but nevertheless the implication exists. Some support for this assumption is presented by Reimers (1963), when considering the survival of liberated hatchery-reared rainbow trout. He reports that those "in the range 0.60–0.70 may be considered marginal in vitality, tiring quickly in stamina tests". The basis of the tests is not clearly indicated, but appears to stem from field observations in an experimental stream (Nielson *et al.*, 1957).

The relation between the condition of the yearling sockeye and their ability to metabolize, and hence perform, was considered by correlation tests relating condition, active metabolism, critical swimming speed, weight, and length (Table VIII). The condition factor ranged from 0.64 to 1.04. The 10°C group had the lowest mean value (0.73±.02) while the 24°C fish had the highest (0.82

TABLE VIII. Correlation coefficients relating condition factor (W/L^3) to various parameters of yearling sockeye salmon (temperature = 15°C). W = wet weight in grams, L = total length in centimetres.

Variates	Correlation coefficients	Significance level		Significant
		P .05	P .01	
Condition × active metabolism	r_{12} −.78	.71	.83	< .05
Condition × critical speed	r_{13} −.27	.71	.83	Not
Condition × length	r_{14} +.36	.71	.83	Not
Condition × weight	r_{15} +.45	.71	.83	Not
Active metabolism × speed	r_{23} +.38	.71	.83	Not
Active metabolism × length	r_{24} −.16	.71	.83	Not
Active metabolism × weight	r_{25} −.24	.71	.83	Not
Speed × length	r_{34} −.56	.71	.83	Not
Speed × weight	r_{35} −.57	.71	.83	Not
Condition × active metabolism (speed constant)	$r_{12\cdot3}$ −.75	.75	.87	.05
Condition × active metabolism (length constant)	$r_{12\cdot4}$ −.77	.75	.87	< .05
Condition × active metabolism (weight constant)	$r_{12\cdot5}$ −.78	.75	.87	< .05

±.04; Table I). There was a significant difference at a $P_{.05}$ level between the extremes but not between the balance.

Condition factor and weight were not significantly related. This point is worth noting since the power *3* for length (L) is arbitrarily used as a generally suitable exponent. If it were unsuitable in the present case a significant difference with weight would have been expected.

The only significant correlation was a negative relation between condition and active metabolism at 15°C ($r = -.78$; $P = .02$). The coefficients for the other four acclimations were all negative but none exceeded −.57 ($P_{.05} = .63$). Given that the fish were equally healthy, the negative correlation would be expected on the basis that the heavier fish contained more stored reserves not involved in active metabolism. Critical speed and condition were not related, nor were active metabolism and speed, which speaks highly of the physical fitness of all the fish independent of plumpness. Partial correlation coefficients were also determined. These did not alter the significance of any relation (Table VIII).

It can be concluded that the stock was indeed a healthy one and that the metabolic rate for unit weight is inevitably lowered for fish with a high condition factor, provided of course they are in good physical condition.

The lack of any significant relation above 15°C is explicable on the basis of oxygen as a limiting factor, masking the relation by restricting the full capacity to metabolize. Fish which had a still lower value than 0.64 for condition factor might well be inferior fish. This points up the need to consider the meaning of "condition factor", which would be particularly valuable if it reflected capacity to survive in nature. Size alone may have some advantage, but if it relates to poor performance it may at times be a greater handicap than advantage.

Fish Composition

Examination of the moisture and lipid fractions of the fish should be revealing in regard to the weight influence on metabolic rate and the condition factor–metabolism relation. The supposition is that variation in active metabolic rate for immature fish of the same weight and age is due to a difference in the proportion of moisture, lipid, and protein[6], and that if the moisture and lipid are subtracted then the variability in metabolic rate per unit weight of the "residue" would be significantly reduced. In addition the respiratory coefficient *b* would approach 1.0, i.e. directly proportional to the mass of residue rather than the 0.8 value of Winberg (1956).

To test this the results for 15°C yearling sockeye have been analysed (Table IX). From the regression equations it is apparent that the slope for wet weight is not significantly different from 1.0 (as might be expected from the lack of a significant correlation between standard metabolic rate and weight — page 1209) nor are those for dry weight and dry weight-less-lipid. The surprising point is that the variability is not reduced since it was thought likely that a major cause of difference would be removed.

[6]Carbohydrate makes up less than 2% (Love, 1957; Fontaine and Hatey, 1953).

TABLE IX. Values for exponent "b" for the equation: $\log Y = a + bX$, where Y = mg O_2 consumed/hr and X = weight (grams), as indicated below. Fiducial limits determined for P = .05 (Goulden, 1952).

X-factor	b-value	Fiducial limits
Wet weight	0.88±.26	0.62–1.14
Dry weight	0.83±.26	0.57–1.09
Dry weight — lipid	0.85±.27	0.58–1.12

In the face of a significant negative correlation between condition and active metabolism the conundrum remains, except to conclude that the moisture and lipid fractions reflect the capacity to metabolize, or are involved in the process in some indirect fashion. The consequence is that the wet weight is as suitable to use as the other weight measures, a point which Zeuthen (1953) was forced to conclude following a study of metabolism and weight in a wide variety of organisms.

One relation of interest that emerged was a highly significant negative correlation between the proportion of lipid and water ($r = -.84$, $P_{.01} = .37$, $n = 44$). Where there was proportionately a lot of fat there was little moisture and vice versa. Thus, although considerable differences in fat and moisture content occurred, they tended to balance out with the result that the dry weight minus lipid paralleled the wet weight.

OXYGEN DEBT

The fact that sockeye were exercised to the exhaustion point presented an opportunity to examine not only the extent of sustained debt, but also the effect of acclimation temperature on this load, the rate of recovery, and the *state* of recovery in terms of capacity to re-perform (Table III).

RECOVERY TIME. The primary phase of recovery in sockeye was rarely characterized by restless movements except at temperatures of 20 and 24°C. The start of spontaneous activity was accompanied by a levelling-off in the decline of metabolic rate, with some increase in metabolism when the movements included turns and roaming. An example of an 11-hr record is given in Fig. 18 in which only the last rate was within 12% of the standard metabolic rate. To assess the significance of return of spontaneous activity, the system of re-imposing the last fatigue-producing velocity was adopted. Most cases were curtailed when the fish demonstrated an ability to perform for as long as the previous fatigue time (Table III). Out of eight cases, only one was unsuccessful; by comparison, the time to fatigue in one successful case was over twice as long as the original time. It is perhaps unsound to make such a comparison as this, since the original test was a prolonged step-type one. It is appropriate, however, to conclude that recovery was sufficient to permit a high level of performance.

A comparison of the times to recovery for each acclimation showed no significant difference between the means. The overall mean, not including the

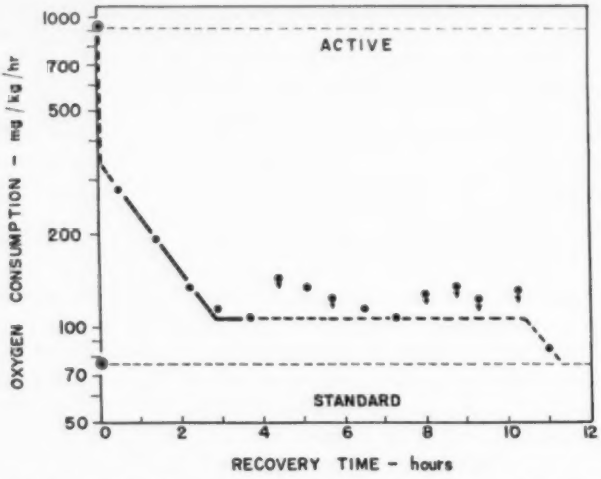


FIG. 18. Eleven-hour record of respiratory metabolism following fatigue in a yearling sockeye (25 cm, 121 g, 15°C). Active and standard rates previously determined from performance studies. The fish was not observed frequently after 5 hr so subsequent elevated points without an arrow may have been accompanied by unnoted spontaneous activity.

uncertain 24°C group, was 191±3.8 min (3.2 hr). This is somewhat faster than the recovery rate for adult coho salmon (*O. kisutch*) following fatigue in an annular chamber (Paulik *et al.*, 1957). Using the method of testing capacity to re-perform, recovery of the coho was approximately 67% complete after 180 min of rest. The rate of recovery was such that completion would be predicted within 5 hr at most; however, only tests at 18–24 hr were conducted beyond the 3-hr recovery stage. These showed complete recovery.

In the extensive experiments of Black *et al.* (1962) on recovery from fatigue in hatchery-reared rainbow trout at 11.5°C, muscle pyruvate was mostly dissipated after 4 hr of recovery, but blood and liver levels of pyruvate and lactate remained elevated for nearly 12 hr. Muscle lactate was less than ½ reduced by 4 hr, continuing to decrease for 8 hr before reaching normal concentrations. Heath and Pritchard (1962) obtained similar times for return of normal levels of blood lactic acid, but report that respiratory metabolism remained elevated beyond 10 hr.

For "trained" rainbow trout Hochachka (1961) did not observe a return of muscle glycogen in less than 18 hr. However, pre-exercise respiration rates were re-established in 4–6 hr after fatigue, a situation not unlike the sockeye recovery. Since the sockeye could re-perform successfully, Hochachka's deduction is pertinent, namely that "all the accumulated lactate need not be oxidized when the oxygen debt has disappeared, but only that it bear a certain relationship to pyruvate, so that metabolic oxidations can return to normal".

SUSTAINED DEBT. The debt replaced up to the start of spontaneous activity was plotted against acclimation temperature (Fig. 19, "overload debt"). For comparison the mean rates of replacement (Fig. 8 and 10) were extrapolated to the respective levels of standard metabolism, thereby making it possible to compute a total sustained debt. The difference between these two levels of debt probably represents the sort of tolerable load readily sustained by the fish. Temperature effect was pronounced. At an optimum of 15°C the total debt (680 mg O_2/kg) exceeded the 5°C level (350 mg O_2/kg) by almost two times. The decline appears to relate to an inability to extract oxygen at an increased rate at higher temperatures, coupled with an elevated standard metabolism. This is revealed by the decreasing slope in the recovery rate above 15°C (Fig. 10).

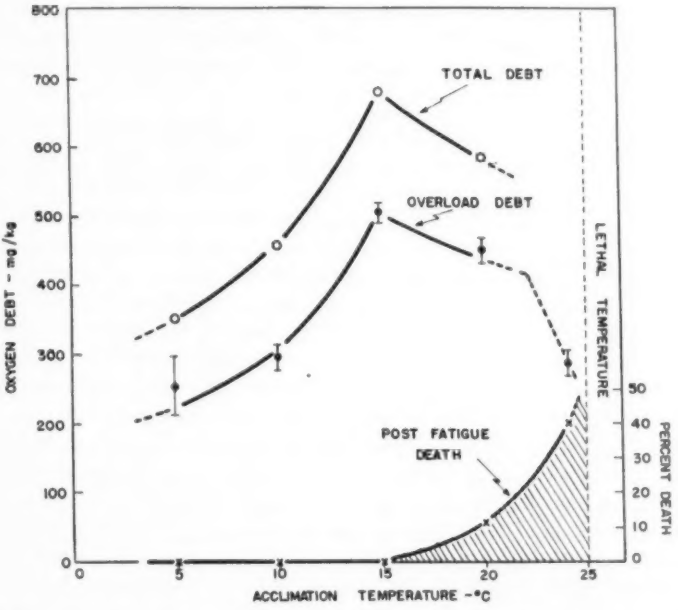


FIG. 19. Magnitude of oxygen debt replaced following fatigue in yearling sockeye at different acclimation temperatures. Amount replaced (mean ±2 S.E.) to start of spontaneous activity labelled "overload debt", and amount calculated to the level of standard metabolism labelled "total debt". Incidence of death during recovery is shown.

Having determined the amount of oxygen debt which young sockeye could sustain at each acclimation temperature, and also the relation between rate of oxygen consumption and swimming speed, it was possible to predict the time-to-fatigue for burst performances. For example, at 10°C the active metabolic rate was 627 mg O_2/kg/hr at a critical speed of 3.65 L/sec (Table I). The calculated demand for swimming at 4.5 L/sec is approximately 1080 mg O_2/kg/hr; a

differential of 453 mg O_2/kg/hr exists. Since a debt of at least 328 mg O_2/kg can be accumulated at this acclimation temperature, the time-to-fatigue would be expected to be about 43 min. At best the observed performance was not more than 8 min (Fig. 12).

The differential can be accounted for by assuming that considerable debt is carried from one sustained swimming stage to another, and that in the speed tests there is already an accumulated debt from excitement and preliminary performance before the final burst. This is a recognized phenomenon in muscular activity of man in which long-distance runners may build up a sizeable debt although not be exhausted at the end of the race (Karpovich, 1959).

To check the possibility of oxygen debt under "normal load" a few experiments were conducted, switching to resting conditions during a sub-fatigue swimming performance. These confirmed the presence of a definite debt, replaced within an hour of recovery. It is apparent that the greatest precautions to avoid complications from oxygen debt have to be used in exploring respiratory metabolism in relation to prescribed activities.

MAXIMUM OXYGEN CONSUMPTION. One comparison of interest turned up from the linearized relation on rate of replacing oxygen debt which permitted extrapolation to the instantaneous metabolic rate immediately following fatigue (Fig. 8 and 18; Table III). This represents the maximum uptake of oxygen during deep opercular ventilation when lying almost motionless in water of 0.1 ft/sec velocity. When swimming, flushing of the gills is achieved usually by holding the mouth and opercula slightly open. Maximum velocities ranged from 1.8 ft/sec (5°C) to 2.5 ft/sec (15°C). One of the signs of approaching fatigue was the onset of irregular gasps. The comparative rates of respiratory metabolism under the two circumstances showed that the maximum achieved while swimming was *twice* that for resting with deep respiration.

These findings are in contrast to those reported by Saunders (1962) for gill irrigation in swimming and resting white suckers, brown bullheads, and carp, when stimulated by low levels of oxygen or high levels of carbon dioxide. In the presence of these stimulating agents the non-swimming fish had the larger respiratory volume. Since oxygen debt probably stimulates respiration in the manner of decreased oxygen, the difference could be one of species characteristics. Alternatively fatigue may be accompanied by cardiac depression or loss of blood volume resulting in circulatory insufficiency. Black *et al.* (1962) have suspected this. In the present experiments, as stated previously, 29% showed a primary or secondary slump in respiration during recovery. However, in the cases not involved with such respiratory irregularities, an inability to increase the rate significantly at temperatures above 15°C has been attributed to limiting oxygen. Furthermore, ability to re-perform within 3 hr is an indication of the integrity of the metabolic and supporting circulatory and excretory systems.

SWIMMING SPEED

PERFORMANCE TIME. To establish a complete fatigue curve, experiments must be continued until a definite "break" in the relation of fatigue time and

velocity is obtained indicating a true sustained capacity. From burst speed studies on trout, dace, and goldfish, Bainbridge (1960) thought that "by 20 seconds the low steady cruising speed seems generally to have been reached", whereas steady performance appeared to require up to 40 min for young sockeye (Brett *et al.*, 1958). Subsequently, Bainbridge (1962) extended the test period to 5 min and still obtained a levelling off in less than 60 sec; data for six trout which fatigued from 32 to 104 min are given but cannot be directly related to the shorter experiments. Swimming performance of immature Atlantic herring has been presented by Boyar (1961) and re-drawn as endurance curves by Blaxter and Holliday (1963). None of these reaches a terminal plateau.

A comparison of the results obtained by Bainbridge (1962) and those for sockeye are presented in Fig. 20. It is apparent that a change in the relation occurs between 0.2–0.4 min (12–24 sec) with a distinct alteration in slope, but not terminating the fatigue curve. Since the mean speeds are plotted in the upper curve involving different species, temperatures, and apparatus the individual records on rainbow trout are included in the lower curve (Bainbridge, 1962). These support the general relation showing the same inflection at about 0.3 min. To complete the fatigue curve the transition to a true sustained speed at about 300 min is included in the figure.

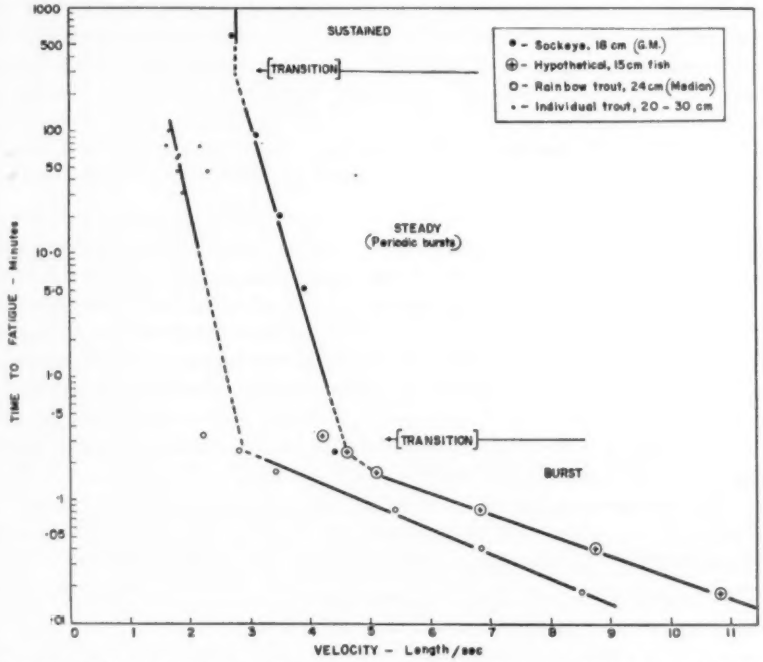


FIG. 20. Fatigue curve for yearling sockeye compared with results obtained by Bainbridge (1960, 1962). Two transition zones (broken lines) appear to exist where variability might be expected to be greatest.

It is very likely that these data represent three stages of availability of fuels for muscular contraction, interrelated with the limiting circumstances of accumulated by-products of anaerobic metabolism and the problem of oxygen supply to the tissues. The rapid fatigue phase (burst) would represent an exhaustion of the available cellular source of energy. The observation by Black *et al.* (1962) that muscle glycogen is reduced to less than one-half the resting level within 2 min with rapid elevation of pyruvate and lactate supports the basis for early collapse when maximum muscular effort is involved. Performance which can be steadily maintained for from 2 to 200 min is more likely to relate to the supply of metabolites delivered by the blood to the muscles and the capacity of the liver to maintain adequate levels from its reserves of glycogen. Hochachka (1961) has shown in a comparison of hatchery and wild trout that liver glycogen levels are dependent on recent feeding and "were reduced to very low levels during transportation" for planting. Finally, beyond 200 min a state of balance must exist between supply and demand, involving a continuous conversion of fat and protein to provide utilizable carbohydrate. This implies that circulation and respiration are not limiting. Indeed this is an obvious conclusion for sustained performance. The middle "link" would appear to be the critical phase where such systemic mechanisms could act as limiting factors.

It is apparent that for sockeye a reliable estimate of sustained speed could not be obtained under a test period of about 5 hr. This may not apply more generally but until explored in other species it remains as one of the reasons why such differences in reported "sustained" speeds occur. The values given for sockeye by Brett *et al.* (1958) were recorded for fork length. If these are converted to total length (by adding 6.4%) and expressed as speed in L/sec the relation for underyearlings (7.4 cm) and yearlings (15.4 cm) is seen in Fig. 21.

SIZE EFFECT. Since form changes with size, the combined effect can be tested by correlating speed with length (Table X). A significant negative correlation was obtained for three of the four acclimations; apparently as the fish grows its *relative* capacity to perform decreases. This was recognized by Bainbridge (1958) for burst speeds. The relation was more pronounced in goldfish than trout. Blaxter and Dickson's (1959) treatment of burst speeds in herring showed the relation between body length (L) and swimming speed (V) to be in the form $V = 7.6\ L^{0.94}$, indicating an almost direct dependence of speed on length. Using the same log–log relation Bainbridge (1960) obtained a variety of slopes for different sustained times (.5–20 sec) with a mean slope of 0.58 for trout. Similar determinations for sockeye using the 1-hr sustained speeds at 15°C resulted in a value of 0.49. There is a suggestion in the goldfish values (Bainbridge, 1960) that low values are associated with longer test times.

The conclusion is that large fish swimming for a long time would have a relatively low ratio of sustained speed to length (L/sec).

TEMPERATURE EFFECT. The effect of temperature on swimming speed, as indicated previously, has been subject to some conflicting reports. These have been resolved by the evidence for the relative temperature-independence of

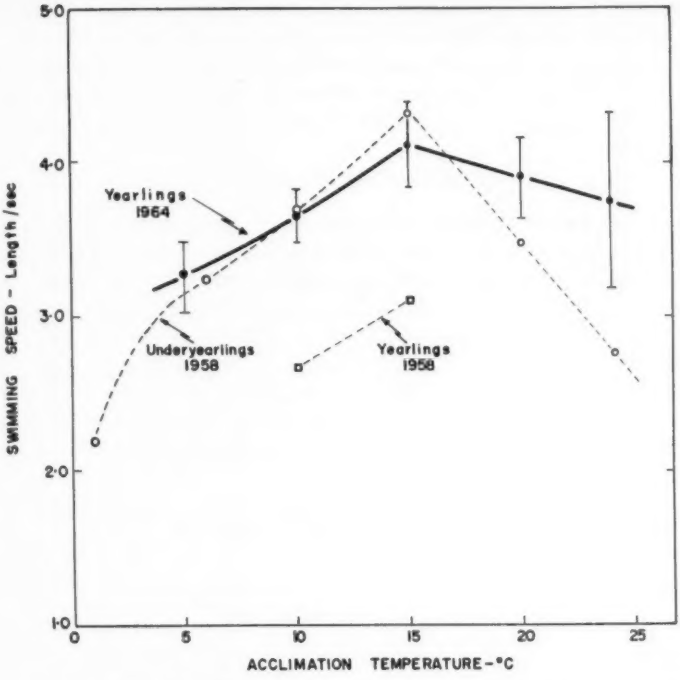


FIG. 21. Relation between swimming speed and acclimation temperature for sockeye tested in a rotating circular trough without an electric screen (1958), and in the respirometer (1964).

burst speeds. The temperature-dependent cruising speeds determined by Brett *et al.* (1958) at various acclimation temperatures have been plotted for comparison with the critical speeds obtained in the respirometer (Fig. 21). A Q_{10} of 1.4 applies to the effect between 5 and 15°C. Some differences exist but the general pattern of temperature effect is comparable. The differences pertain to lower performance (about 25%) among the yearlings tested in the circular trough.

TABLE X. Correlation coefficients between critical swimming speed (sustained for 60 min) and length, for various acclimation temperatures.

Acclimation temperature	Correlation coefficient	Significance
(°C)	(r_{xy})	(*P value*)
5	−.71	$P < .05$
10	−.51	$P \approx .1$
15	−.88	$P < .01$
20	−.86	$P < .01$

Underyearlings, however, achieved the same relative performance (L/sec) in the circular trough as the yearlings did in the respirometer for 5, 10, and 15°C. At lower and higher temperatures there was a significant reduction in the cruising speed, probably due to a behavioural difference requiring a stronger stimulus than was applied in the circular trough to achieve the performance induced in the respirometer.

GENERALIZED RELATIONS

Some of the factors which govern the rate of metabolism and set limits to its magnitude are apparent in the foregoing presentation. Earlier work on yearling sockeye set forth the limits which temperature sets for survival. Within these boundaries the metabolic rates for various levels of activity have been illustrated (Fig. 13). With the emphasis of the effect of activity on metabolism, the relation has been drafted on arithmetic axes in the form of Fig. 22. Upper and lower lethal temperatures provide the boundaries at the top and bottom of the figure. Limits of activity, from resting states to temperature-dependent critical speeds, provide the remaining boundaries, except for the apex which

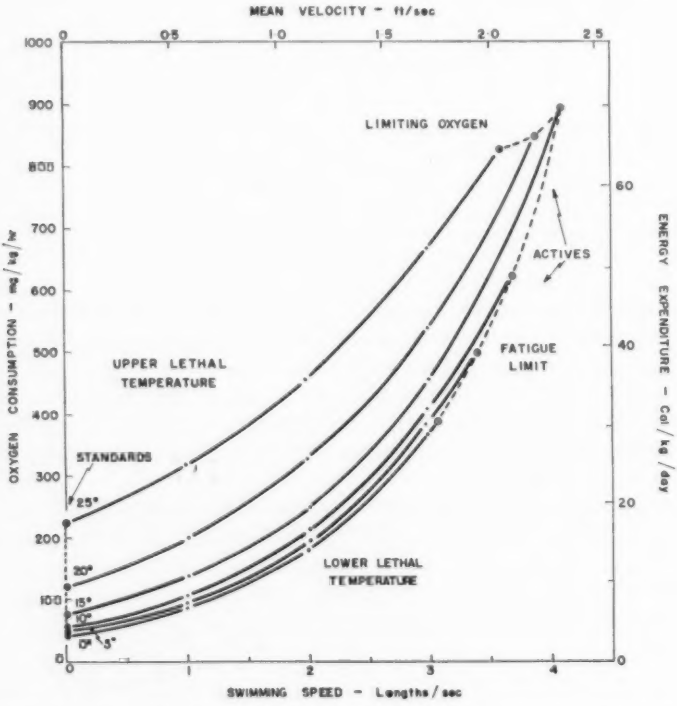


FIG. 22. General relation between oxygen consumption and swimming speed for yearling sockeye salmon in air-saturated fresh water, showing the factors governing the limits of performance.

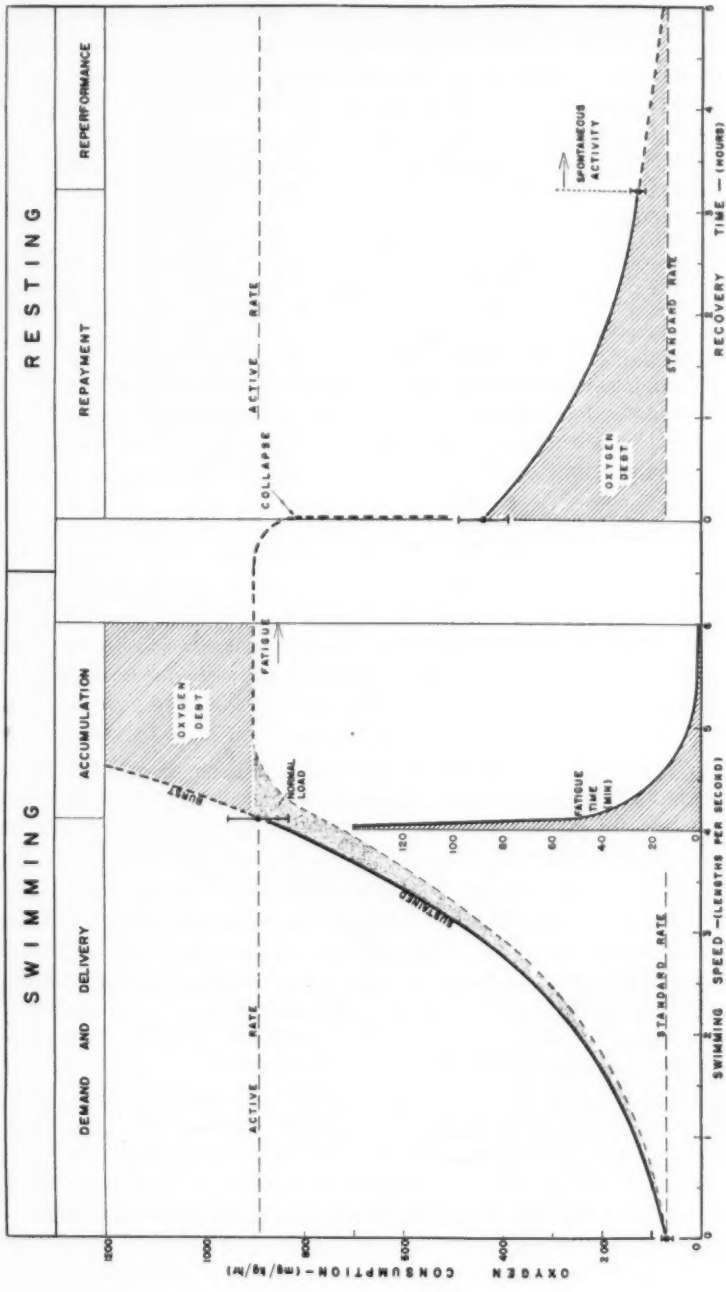


FIG. 23. General relation of oxygen consumption, swimming speed, fatigue time, oxygen debt, and recovery time for an 18-cm, 50-g yearling sockeye performing in air-saturated fresh water at 15°C.

appears to be limited by environmental oxygen. It is seen that *external* factors provide the limits on all sides except the fatigue boundary. It would appear that some temperature-dependent factor of *internal* origin is setting this limit. As has been suggested, in all likelihood this is the supply of metabolic fuels together with the influence of anaerobic products.

The interrelations of oxygen uptake, performance, fatigue times, and oxygen debt repayment are depicted in Fig. 23. Although derived from the total data and distilled into one figure, the relation is within the confidence limits obtained for 15°C-acclimated 50-g sockeye. Broken lines indicate the extrapolated path of increasing oxygen requirement above the active metabolic rate which forces the fish into a cumulative oxygen debt, inducing collapse. The length of time which the excessive rate can be maintained is defined by the fatigue curve. Following exhaustion, deep ventilation in the non-swimming fish for about 3 hr pays off the immediate oxygen debt leaving the fish free to commence spontaneous activity and to re-perform at a successful burst level again. It must be concluded that although the fish is unlikely to be back to resting levels of blood constituents, the capacity to re-perform certain swimming feats ensures a reinstatement of survival capacity.

SUMMARY AND CONCLUSIONS

1. The relation between respiratory metabolism and swimming speed in young sockeye salmon was found to be exponential, described by the general equation $Y = ae^{bX}$, where Y = rate of oxygen consumption (mg O_2/kg/hr) and X = speed (L/sec). The relation applied to all acclimation temperatures from 5°C to 24°C. Values for a ranged from 1.61 to 2.29, and those for b from 0.34 to 0.17.

2. At 5°C the standard metabolic rate was 41 ± 3.2 mg O_2/kg/hr which rose to 196 ± 13 at 24°C. From the basic equation ultimate minimum and maximum levels of 36 mg (0°C) and 200 mg (25°C) were derived, a maximum difference of approximately $5\frac{1}{2}$ times.

3. Active metabolism rose from 514 ± 31 mg O_2/kg/hr at 5°C to a maximum of 895 ± 49 mg O_2/kg/hr at 15°C, with some decrease at higher temperatures.

At temperatures up to 15°C active rates were about 10–12 times the standard level. Above 15°C the ratio fell to about 4 times the standard rate for an acclimation temperature of 24°C. The combined action of temperature and activity elevated respiratory metabolism by a factor of 22 times, equal to the influence of activity on metabolic rate in many mammals.

4. The general level of standard metabolism, supported by evidence from recent literature, is sufficiently below that reported in earlier literature to suggest that excitability has not been accounted for sufficiently to provide an accurate measure of the standard rate. In addition, the high active levels indicate that this parameter has possibly not been determined in its maximum expression. In consequence, calculations based on these indices could be in considerable error.

5. A near linear transformation for the effect of temperature on locomotor metabolism was obtained by relating the logarithm of the swimming requirement *less* the standard rate (locomotor scope) to acclimation temperature. The slopes of the lines decreased with increasing speed, approaching 0 at 4.2 L/sec.

It can be concluded that burst speeds of this level and above are virtually independent of temperature, placing the poikilotherm on a common basis with the homeotherm in this regard.

6. In air-saturated fresh water, oxygen became a limiting factor for active metabolism above 15°C in one group of yearling sockeye. In consequence any reduction in saturation could be expected to further reduce maximum activity above this temperature.

7. Within the range of weight studied (25–130 g) there was no significant correlation between weight and standard or active metabolism at any acclimation temperature, except at 15°C where, by including some underyearlings, a range of 8–130 g was provided. The slope of this line for standard metabolism was $0.88 \pm .26$. The error is such that a slope of 1 could apply throughout.

8. Despite a range in condition factor of 0.64–1.04, only the 15°C group showed a significant correlation between plumpness and active metabolic rate ($r = -.78$; $P = .02$).

Studies on the composition of the fish did not support an expected improved relation between weight and active metabolism by using dry weight minus lipid. A high negative correlation between the relative proportion of lipid and water ($r = -.84$; $P < .01$) provided a partial explanation for the results.

It can be concluded that wet weight was as useful a basis for expressing metabolic rate as either dry weight or dry weight minus lipid.

9. The rate of replacement of oxygen debt following fatigue was found to be exponential with time in the majority of cases. Irregularities occurred in the form of primary or secondary slumps. These were more frequent at temperatures of 20 and 24°C, where post-fatigue death occurred in from 10% to 40% of cases.

Time to return of spontaneous activity was 191 ± 3.8 min, independent of acclimation temperature. At this stage of recovery successful re-performance of the fatigue velocity was possible.

10. The *extent* of debt sustained at the time of fatigue, however, was influenced by acclimation temperature, rising from 252 ± 20 mg O_2/kg at 5°C to a maximum of 504 ± 6 mg O_2/kg at 15°C.

This represents the "overload" debt replaced by the time of the start of spontaneous activity. Total debt, determined by extrapolation to standard metabolism, was about 30% greater. The difference was considered to represent the normal load, demonstrated by a determinable debt present at sub-fatigue velocities.

11. Fatigue curves determined at 10°C were linearized by relating the logarithm of the geometric mean time-to-fatigue to the swimming speed. Two breaks in the relation appear to exist, one between 200 and 300 min defining the

sustained speed and the other at about 20 sec (from data of Bainbridge) where only burst speeds occur.

The geometric mean fatigue time and time-to-50%-fatigue (FT_{50}) determined by plotting log time-to-fatigue against per cent fatigued (probits) were comparable. The latter approach provides a useful basis for comparative studies of performance under different environmental conditions and allows the use of data where not all the fish fatigue by the end of the test time.

ACKNOWLEDGMENTS

The extent to which it has been possible to make relatively rapid progress in these studies stems from the stimulation and consultation which Drs F. E. J. Fry and E. C. Black have continued to provide in the field of respiratory metabolism. The metabolic problems for Pacific salmon with their extensive migrations and consequent large energy demands have received increased attention as a result of Dr W. A. Clemens' efforts to provide for biochemical studies on energy expenditure. It is a pleasure to acknowledge these sources of inspiration.

The diligence and hydrodynamic insight of Mr John Mar of the Pacific Naval Laboratories brought the biological requirements for a tunnel respirometer into an effective, precision instrument. The excellence of the design continues to provide an unusual opportunity for research.

Throughout the many tedious hours of preparation, operation and recording required to obtain the data, Mr D. B. Sutherland has faithfully persevered in all technical matters. His ability and patience have meant much to the successful completion of the project.

The determinations of dry weights and lipid fractions were made by Mr C. T. Shoop, who also assisted in many of the statistical calculations. This help is gratefully acknowledged.

REFERENCES

ALDERDICE, D. F., J. R. BRETT AND D. B. SUTHERLAND. 1964 (in press). Design of small holding tank for fish. Canadian Fish Culturist.

BAINBRIDGE, RICHARD. 1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *J. Exp. Biol.*, **35**(1): 109–133.

1960. Speed and stamina in three fish. *Ibid.*, **37**(1): 129–153.

1962. Training, speed and stamina in trout. *Ibid.*, **39**(4): 537–556.

BASU, S. P. 1959. Active respiration of fish in relation to ambient concentrations of oxygen and carbon dioxide. *J. Fish. Res. Bd. Canada*, **16**(2): 175–212.

BEAMISH, F. W. H. 1964a. Influence of starvation on standard and routine oxygen consumption. *Trans. Amer. Fish. Soc.*, **93**(1): 103–107.

1964b. Respiration of fishes with special emphasis on standard oxygen consumption. II. Influence of weight and temperature on respiration of several species. *Canadian J. Zool.*, **42**: 177–188.

BEAMISH, F. W. H., AND P. S. MOOKHERJII. 1964. Respiration of fishes with special emphasis on standard oxygen consumption. I. Influence of weight and temperature on respiration of goldfish, *Carassius auratus* L. *Canadian J. Zool.*, **42**: 161–175.

BLAXTER, J. H. S., AND W. DICKSON. 1959. Observations on the swimming speeds of fish. *J. Cons. Expl. Mer*, **24**: 472–479.

BLAXTER, J. H. S., AND F. G. T. HOLLIDAY. 1963. The behaviour and physiology of herring and other clupeids, pp. 261–393. *In* F. S. Russell, [ed.] Advances in marine biology, Vol. I. Academic Press, N.Y.

BLAZKA, PAVEL. 1960. Maximum and active metabolism in fish, pp. 27–29. *In* Studies on the comparative physiology of metabolism. Babak's Collection, Prague.

BLAZKA, P., M. VOLT AND M. CEPELA. 1960. A new type of respirometer for the determination of the metabolism of fish in an active state. *Physiol. Bohemoslov.*, **9**: 553–558.

BOYAR, H. C. 1961. Swimming speed of immature Atlantic herring with reference to the Passamoquoddy Tidal Project. *Amer. Fish. Soc.*, **90**(1): 21–26.

BRETT, J. R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. *J. Fish Res. Bd. Canada*, **9**(6): 265–323.

1962. Some considerations in the study of respiratory metabolism in fish, particularly salmon. *Ibid.*, **19**(6): 1025–1038.

1963. The energy required for swimming by young sockeye salmon with a comparison of the drag force on a dead fish. *Trans. Royal Soc. Canada*, Vol. 1, Ser. IV, pp. 441–457.

BRETT, J. R., AND D. F. ALDERDICE. 1958. The resistance of cultured young chum and sockeye salmon to temperatures below 0°C. *J. Fish Res. Bd. Canada*, **15**(5): 805–813.

BRETT, J. R., M. HOLLANDS AND D. F. ALDERDICE. 1958. The effect of temperature on the cruising speed of young sockeye and coho salmon. *J. Fish. Res. Bd. Canada*, **15**(4): 587–605.

BRETT, J. R., AND D. B. SUTHERLAND. MS, 1964. Respiratory metabolism of pumpkinseed (*Lepomis gibbosus*) in relation to swimming speed at 20°C. MS, Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C.

CARLANDER, K. D. 1950. Handbook of freshwater biology. Wm. C. Brown, Iowa, 281 pp.

EVANS, R. M., R. C. PURDIE AND C. P. HICKMAN, JR. 1962. The effect of temperature and photoperiod on the respiratory metabolism of rainbow trout (*Salmo gairdneri*). *Canadian J. Zool.*, **40**(1): 107–118.

FISHER, R. A. 1948. Statistical methods for research workers. 10th ed., Oliver & Boyd, Edinburgh, 384 pp.

FOLCH, JORDI, M. LEE AND G. H. S. STANLEY. 1957. A simple method for the isolation and purification of total lipids from animal tissues. *J. Biol. Chem.*, **226**(1): 497–509.

FONTAINE, M., AND J. HATEY. 1953. Contribution à l'étude du métabolisme glucidique du saumon (*Salmo salar* L.) à divers étapes de son développement et de ses migrations. *Physiol. Comparata et Oecol.*, **3**: 37–52.

FRY, F. E. J. 1957. The aquatic respiration of fish, pp. 1–63. *In* M. E. Brown, [ed.] Physiology of Fishes, Vol. I. Academic Press, New York.

GIBSON, E. S., AND F. E. J. FRY. 1954. The performance of the lake trout, *Salvelinus namaycush*, at various levels of temperature and oxygen pressure. *Canadian J. Zool.*, **32**: 252–260.

GOLDSTEIN, S. 1938. Modern developments in fluid dynamics. Vol. I, 330 pp. Oxford.

GOULDEN, C. H. 1952. Methods of statistical analysis. John Wiley & Sons, New York, 467 pp.

HICKMAN, CLEVELAND P., JR. 1959. The osmoregulatory role of the thyroid gland in the starry flounder, *Platichthys stellatus*. *Canadian J. Zool.*, **37**(6): 997–1060.

HOCHACHKA, P. W. 1961. Liver glycogen reserves of interacting resident and introduced trout populations. *J. Fish. Res. Bd. Canada*, **18**(1): 125–135.

IDLER, D. R., AND W. A. CLEMENS. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart Lakes. *Int. Pacific Salmon Fish. Comm., Prog. Rept.*, 80 pp.

JOB, S. V. 1955. The oxygen consumption of *Salvelinus fontinalis*. *Publ. Ontario Fish. Res. Lab.*, No. 73, 39 pp.

KARPOVICH, P. V. 1959. Physiology of muscular activity. 5th ed. W. B. Saunders Co., London. 368 pp.

LOVE, R. M. 1957. The biochemical composition of fish, pp. 401–418. *In* M. E. Brown, [ed.] Physiology of Fishes, Vol. I. Academic Press, New York.

MAR, JOHN. 1959. A proposed tunnel design for a fish respirometer. Tech. Memo. 59-3, Pacific Naval Laboratory, D. R. B., Esquimalt, B.C.

NIELSON, R. S., N. REIMERS AND H. D. KENNEDY. 1957. A six-year study of the survival and vitality of hatchery-reared trout of catchable size in Convict Creek, California. *California Fish and Game*, **43**(1): 5–42.

PAULIK, G. J., A. C. DELACY AND E. F. STACY. 1957. The effect of rest on the swimming performance of fatigued adult silver salmon. *Univ. Washington, School of Fisheries, Tech. Rept.* No. 31, 24 pp.

REIMERS, NORMAN. 1963. Body condition, water temperature, and over-winter survival of hatchery-reared trout in Convict Creek, California. *Trans. Amer. Fish. Soc.*, **92**(1): 39–46.

SAUNDERS, R. L. 1962. The irrigation of the gills in fishes. II. Efficiency of oxygen uptake in relation to respiratory flow activity and concentrations of oxygen and carbon dioxide. *Canadian J. Zool.*, **40**(5): 817–862.

SPOOR, W. A. 1946. A quantitative study of the relationship between activity and oxygen consumption of the goldfish, and its application to the measurement of respiratory metabolism in fishes. *Biol. Bull.*, **91**: 312–315.

WINBERG, G. G. 1956. [Rate of metabolism and food requirements of fishes.] Belorussian State University, Minsk. 251 pp. [FRB Translation Series, No. 194].

WOHLSCHLAG, D. E. 1957. Differences in metabolic rates of migratory and resident freshwater forms of an Arctic whitefish. *Ecology*, **38**(3): 502–510.

WOHLSCHLAG, D. E., AND R. O. JULIANO. 1959. Seasonal changes in bluegill metabolism. *Limnol. Oceanog.*, **4**(2): 195–209.

ZEUTHEN, E. 1953. Oxygen uptake as related to body size in organisms. *Quart. Rev. Biol.*, **28**(1): 1–12.

APPENDIX

1 ft/sec = 0.305 m/sec = 0.682 mile/hr

1 cfs = 28.3 l/sec = 449 gal/hr

1 L/sec = 1 total fish-length/sec

1 mg O_2/l = 0.70 cc O_2/l = 1 ppm

1 Cal/kg/day = 12.9 mg O_2/kg/hr (assuming an average oxycalorific equivalent of 4.75 Cal/l O_2)

5°C = 41°F; 10°C = 50°F; 15°C = 59°F; 20°C = 68°F; 24°C = 75°F

Ocean Migrations of Pacific Salmon[1]

By Ferris Neave

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Sockeye salmon (*Oncorhynchus nerka*), pink salmon (*O. gorbuscha*), and chum salmon (*O. keta*) commonly return to their places of origin from distant high-seas areas. Maturing fish closely associated at high-seas localities travel in many different directions to their respective destinations. They also travel from many different high-seas localities to a common coastal area. Prior to their return to inshore waters, pink salmon perform ocean journeys which are associated with changes in temperature and which do not necessarily represent a direct approach to a spawning area. The ocean journeys of both juvenile and maturing salmon are largely independent of currents. Homing is not thought to be commonly accomplished by random or near-random ocean travel or by extensive searching of coastlines. It is suggested that ability to set a compass course, using a celestial feature, is insufficient to account for the indicated performance and that some form of bico-ordinate navigation may be required.

INTRODUCTION

For many years the long migrations of Pacific salmon have invited speculation on the means whereby these journeys are timed and directed. Dr W. A. Clemens is among the investigators who have shown a sustained interest in this subject. He reported some of the earliest ocean tagging experiments conducted on salmon in British Columbia waters and in a later paper (Clemens, 1951) he has discussed the problems of route-finding with particular reference to the sockeye salmon of the Fraser River. Within the last decade increased knowledge of the vast ocean areas inhabited by salmon and the great distances which are commonly traversed without benefit of landmarks has tended to enlarge the field for speculation and inquiry. A recent theoretical treatment of certain aspects of salmon migration has been provided by Saila and Shappy (1963). The present paper will not offer a satisfactory explanation of the mechanism involved in these migrations. Its purpose is to present certain facts and inferences (gathered mainly from field observations) which I believe should be taken into account in formulating theories and which may suggest directions in which further observations and experiments can be made.

While it is assumed that there is a basic similarity in the problems of migration faced by all salmon which venture far into the ocean, and in the means whereby these problems are met, the present notes are based primarily on data relating to sockeye salmon (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*). A few references are also made to chum salmon (*O. keta*). Mostof the data used have been obtained by investigators working under the auspices of the research

[1]Received for publication May 21, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

programs of the member nations of the International North Pacific Fisheries Commission. Considerable use has been made of data obtained in extensive fishing and tagging operations conducted by Canadian vessels throughout the Gulf of Alaska in 1962 and 1963.

HOMING OF SALMON FROM THE HIGH SEAS

In the following discussion the assumption is made that those anadromous salmon which survive to maturity return with a high degree of constancy to the freshwater areas in which they originated. It is not considered necessary to review in detail the extensive evidence for this belief, which incidentally forms a main basis for current management practices and international agreements restricting the fishing of salmon in the ocean. In general this evidence is provided by the following kinds of data: (a) The adult fish returning to a particular stream, watershed, or inshore coastal area commonly exhibit a regular pattern of timing, and sometimes of morphological characteristics or special parasites, which distinguish them from fish associated with other watersheds or inshore areas. (b) The marking (by fin-clipping) of seaward-going migrants has resulted in the recovery in the same streams, after an appropriate period of ocean life, of many adult fish bearing the same marks while few or none in these experiments have been recovered in other streams. (c) The complete or nearly complete absence of pink salmon in alternate years in some areas indicates that there is no large-scale immigration into these areas by fish originating in other regions. Similarly, the regular occurrence at 4-year intervals of the great dominant runs of sockeyes to the Fraser River cannot be explained except on the basis of an extremely strong homing tendency.

The above-mentioned kinds of evidence relate primarily to the fish that actually return to a given stream or local area. Brief reference can be made to suggestions that these returning fish may consist to a large extent of individuals which have remained relatively near to a coastline during their marine life and/or those which, after visiting areas remote from land, have been fortunate rather than perspicacious in their direction of migration: in short, that many of the salmon which attain an advanced stage of maturity in regions far from land are lost at sea through inability to find their way "home".

It is nevertheless clear that most of the salmon which return to fresh water (at least in the cases of sockeye, pink, and chum salmon) have in fact come from the high seas. For example, widespread fishing surveys by research vessels have shown that in winter and spring maturing sockeyes of the Gulf of Alaska are mainly concentrated in a rather well-defined area far from land, with very few inhabiting the waters within several hundred miles of the coastline. During the period from mid May through July the adult populations of this distant area dwindle to insignificance as the familiar runs appear in coastal waters. Similarly, the pattern of distribution of maturing pink and chum salmon shows well-marked movement from high-seas to coastal areas (Manzer *et al.*, 1963). The well-ordered direction and timing of the movements toward the appropriate spawning grounds can be illustrated by the practical experience of the Japanese commercial

high-seas fishery which, beginning in May in the Aleutian area, moves westward with the progress of the season, accompanying the movement of salmon from mid ocean toward the Asian coasts. There can be little doubt of the essential completeness of the shoreward migration of maturing fish. At the same time this evacuation of the high seas is not a random affair since, as already noted, the salmon reaching particular coastal regions frequently exhibit characteristic features separating them from other populations of the same species.

Tagging experiments have shown the presence in the central and western Gulf of Alaska of many maturing chum salmon which subsequently migrated to far-northern coastal areas of Alaska and the USSR. All these recovered fish had been tagged prior to June 15. Fish tagged after this date were only recovered from localities within the Gulf. Similarly, maturing sockeyes which from subsequent tag recovery or from their harbouring of the cestode *Triaenophorus* were identified as Bristol Bay fish, were present in spring as far east as 143°W long but were not found east of 160°W after mid June (Margolis, 1963).

The general picture presented by seasonal changes in distribution and local abundance, by tagging data, and by the arrival of concentrations of fish in well-defined coastal areas, is of extensive ocean feeding grounds which are evacuated in a chronological order by the salmon proceeding to different spawning areas.

MINGLING OF POPULATIONS IN THE HIGH SEAS

Acceptance of the validity of the general rule that maturing Pacific salmon return to their places of origin raises the question whether the various stocks or populations tend to occupy separate parts of the ocean.

It can be stated at once that there is commonly a great deal of intermingling between populations of widely different places of origin. Figure 1 shows, in outline, areas in the Gulf of Alaska occupied by maturing sockeye salmon of several different stocks at a season (April 9 to May 24, 1962) prior to their shoreward migration. The identification of these stocks was based on subsequent coastal recoveries of fish tagged during the indicated period. The degree to which a common territory was occupied by fish of diverse origins could have been further emphasized by the inclusion of other stocks which have been omitted for the sake of clarity. Even more striking has been the finding that chum salmon tagged within a relatively small region of the western Gulf of Alaska in April and May 1962, yielded returns from localities representing practically the whole known geographical range of the species (Japan, USSR, and North American localities from the Arctic Ocean to Washington State).

The above examples refer to areas of considerable size and time-periods of several weeks. A more intimate degree of intermingling is illustrated in Fig. 2. This shows the distribution of recoveries of tagged sockeyes all of which were caught in a single longline set made in the middle of the Gulf of Alaska on April 27, 1962. These recoveries show that fish which were in close association at the tagging point went to a majority of the North American coastal areas in

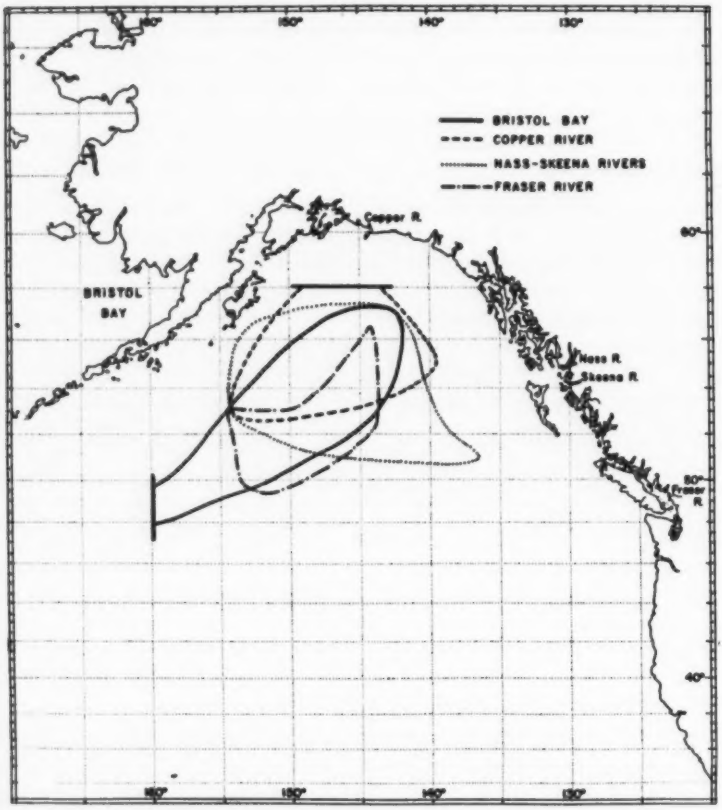


FIG. 1. Ocean areas occupied by maturing sockeye salmon, associated with various coastal areas, within the period April 9 to May 24, 1962. (Straight lines represent boundaries of region investigated.)

which sockeye fishing is extensively practised. The distance by sea between the most widely separated recovery points (Bristol Bay and Fraser River) is approximately 2000 miles. Individual fish made minimum journeys of from 350 to 1000 miles which in some instances varied in direction by 180°.

An example of divergent courses taken by pink salmon caught in a single set is given in Fig. 3. Many similar instances could be presented[2].

[2]While the mingling of stocks is a prevalent feature of high-seas distribution, a degree of segregation was indicated for pink salmon which migrated to the central part of the British Columbia coast in 1962. In April and May these fish occupied an ocean area within about 200 miles of the Washington and southern British Columbia coasts in which very little admixture of other stocks was demonstrated. Later in the season, when the fish had moved farther north, they were found in company with other stocks.

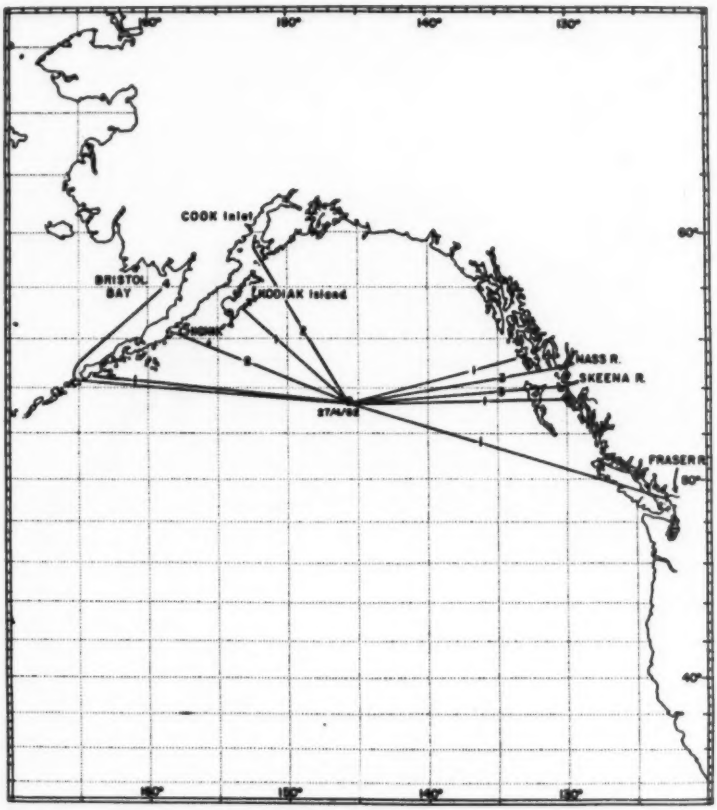


FIG. 2. Distribution of recovered sockeye salmon tagged at the same place and time.

THE APPROACH TO COASTAL LOCALITIES

While the divergence of fish in many directions from a high-seas point is striking, the convergence of a spawning population on a single coastal area from a diversity of directions is also noteworthy. The extensiveness of the ocean region that may be occupied by the maturing fish of a given watershed or small coastal area has been illustrated elsewhere (Anon., 1964) in diagrams showing the ocean distribution of the tagged salmon which returned to each of many such coastal localities from the high seas of the Gulf of Alaska in 1962. (Total tag recoveries from the Gulf operations in that year included 683 sockeyes, 558 pinks, and 116 chums.) These data in general showed that salmon reached their destinations from ocean points representing a wide angle. However, since the taggings were made over a period of many weeks, some of the differences in direction could have been due to movements of fish from one tagging point to another during this period. Figure 4 and 5 represent cases in which taggings

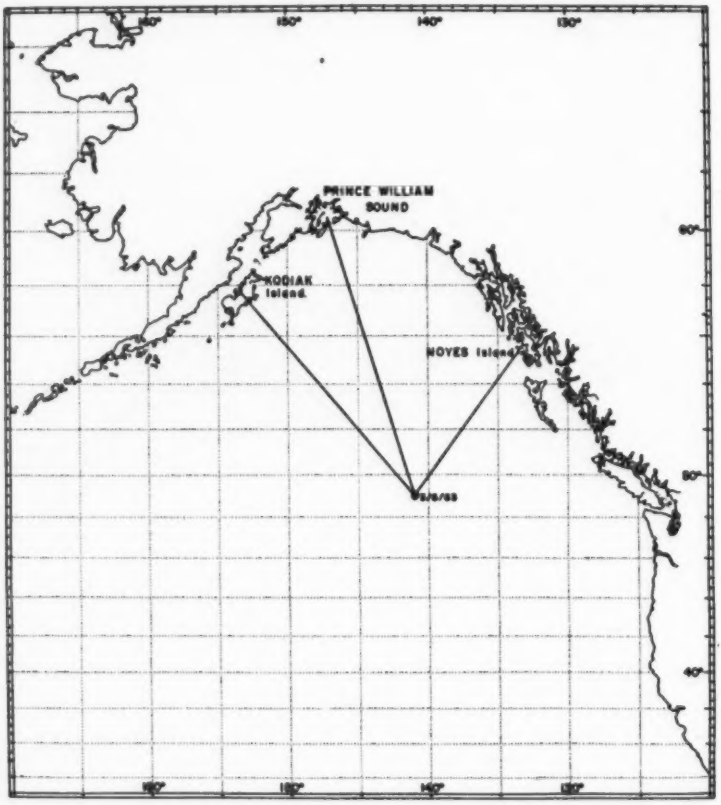


FIG. 3. Distribution of recovered pink salmon tagged at the same place and time.

were made at different places on the same or nearly the same date, thus indicating broad territories occupied *simultaneously* by maturing salmon associated with a particular coastal area.

Figure 4 shows high-seas positions from which sockeyes, tagged within a 3-day period, migrated to the Copper River, Central Alaska. The fish at the two most widely separated localities (about 450 miles apart) were tagged on the same day. One fish from each of these two points was also recovered on the same day (May 28) at the Copper River delta. The other fish from the western locality was recovered at a later date (July 2) some 75 miles up the river. The remaining fish from the eastern location was reported from the Copper River delta "early in June".

An even wider spread of tagging localities for pink salmon which converged on Kodiak Island is shown in Fig. 5. The localities plotted are of fish which were tagged within the period of June 20–22, 1962. The total east–west distance

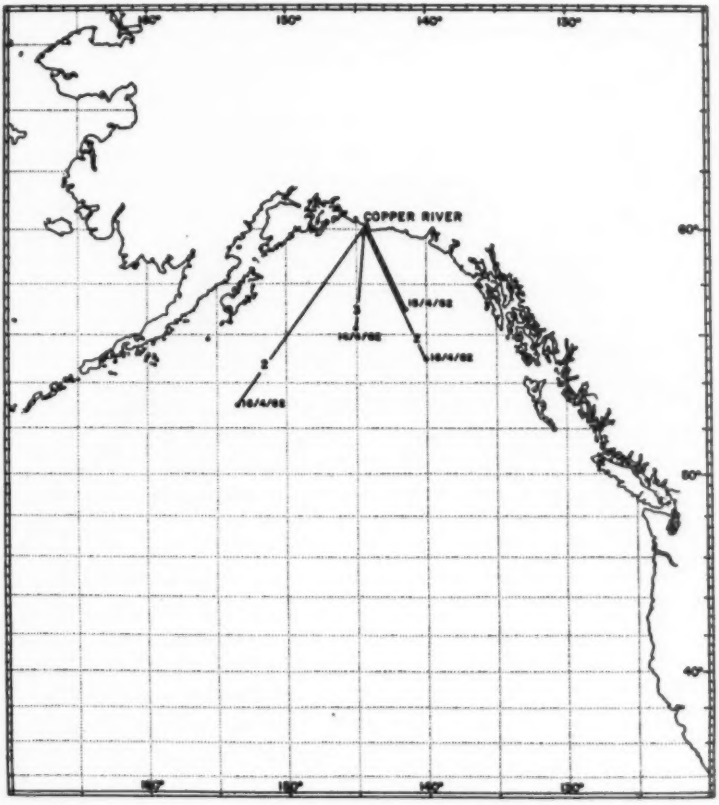


FIG. 4. Ocean localities from which sockeye salmon, tagged on or near the same date, travelled to the Copper River, Alaska.

covered by these taggings was approximately 800 miles. The salmon were recovered from bays and streams of Kodiak Island in late July and August. The minimum distances covered by the individual fish between tagging and recovery areas varied from 250 to 800 miles.

Since it has sometimes been thought that migration in coastal waters involves an essentially different mechanism from direction-finding on the high seas, the following brief notes are offered regarding the "offshore" and "inshore" journeys of homeward-bound salmon.

Great numbers of sockeye and pink salmon bound for the Fraser River travel the full length of Vancouver Island, from northwest to southeast, following the west coast of the Island or threading the narrow passages between Island and mainland. On the other hand pink salmon are also known to travel northward along the British Columbia coast. Fish of this species tagged near the

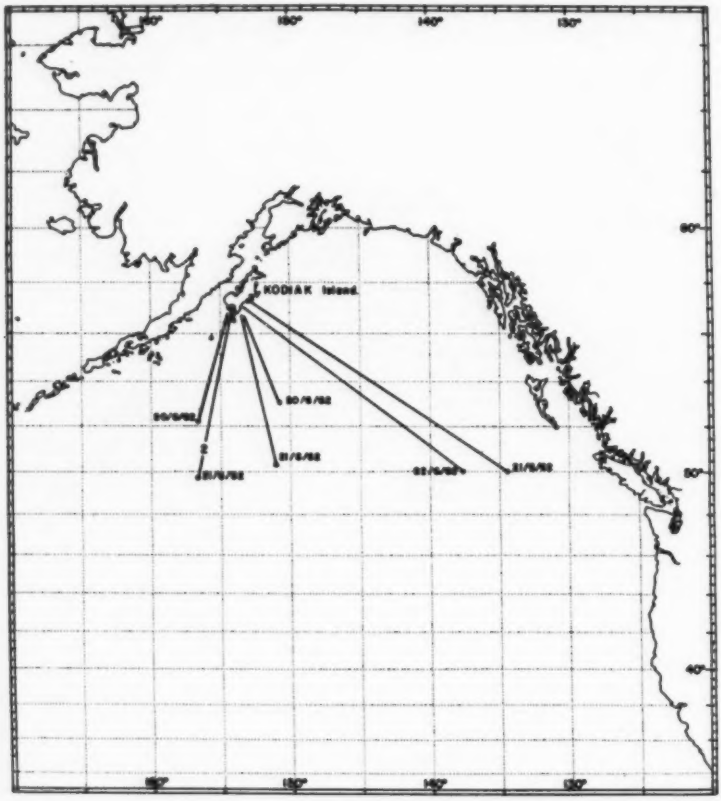


FIG. 5. Ocean localities from which pink salmon, tagged on or near the same date, travelled to Kodiak Island, Alaska.

southern boundary of the province have yielded many recoveries from coastal localities farther north and other individuals have been known to travel from the south end of the Queen Charlotte Islands to points some 450 miles distant in southeastern Alaska. These and other instances which could be adduced indicate that salmon do at times make journeys of up to several hundred miles in coastal waters.

On the other hand there are indications that many maturing fish reach their freshwater destinations by a more or less direct route from the high seas. The great majority of the sockeyes travelling to Rivers and Smith Inlets appear to funnel inshore through Queen Charlotte Sound and taggings have failed to show the presence of these fish in inshore waters south of 50°N or north of 52°N. Even the Fraser River sockeyes, which make relatively long coastal journeys, have not been identified in coastal waters from farther north than the southern

end of the Queen Charlotte Islands (52°N). In the northern coastal regions of the Gulf of Alaska both sockeyes and pinks appear to make a rather direct approach from the high-seas, without extensive coastal migrations.

In short, the homeward migration of salmon from the high seas may or may not include an extensive journey paralleling a coastline.

The migration routes taken by salmon in the final stages of their marine life should be considered in relation to their distribution and movements prior to this period. The total period of life in the ocean is commonly 1, 2, 3, or even more years. The final migration to a spawning area may take only a few weeks[3].

Surveys made in the Gulf of Alaska in 1962 and 1963 showed that in April and May (i.e. well prior to the spawning period) maturing sockeyes were concentrated in the central part of the Gulf, far from land (Fig. 1). For the Fraser River fish occupying the central and northern part of this region the routes along the coasts of Vancouver Island represent approximately the straightest course to the spawning areas. Fish migrating to the Fraser from the southernmost part of this extensive feeding ground apparently swing somewhat to the north before making a landfall, thus avoiding an ocean area of high temperature from which salmon of all species are almost absent after June. The boundary of this avoided area is approximately represented by a surface isotherm of 14 or 15°C (Manzer *et al.*, 1963; Neave and Hanavan 1960; see also figures 6, 12, 18 in Anon., 1964 and compare with figure 12c in Dodimead *et al.*, 1963).

The coastal movements of pink salmon should also be viewed in relation to the previous ocean distribution of the species. In April the pink salmon which eventually reach streams of the central part of the British Columbia coast are mainly off the Vancouver Island and Washington coasts, well to the south of their spawning areas, in relatively warm water. As the season progresses they spread northwestward, and, in general conformity with the shift of the isotherms, by July many of the fish are well to the north and west of their ultimate destinations. Fish tagged at different stages of this northward migration of course show different directions of approach to their spawning areas — from south, west, or northwest. On the other hand the populations proceeding to the more northerly coasts of the Gulf, also starting from southern latitudes, pursue a less varied course. The fact that many pink salmon of the more southerly populations "overshoot" their final destinations does not imply that they are "off-course". Similar northwestward movements in the Gulf of Alaska at the same season are made by various strictly marine fishes such as the pomfret (*Brama raii*), jack mackerel (*Trachurus symmetricus*), and blue shark (*Prionace glauca*) (Neave and Hanavan, 1960). The seasonal migration of chum salmon from the central north Pacific toward the Asian coast includes immature as well as maturing

[3]For example, it has been shown that sockeyes of the Skeena and Nass Rivers in 1962 occupied an ocean area in the central Gulf of Alaska from April onward (Neave *et al.*, MS, 1963). They were not found west of 154° W long at any time. However, fish were still present near the western boundary of this area as late as July. One such fish, tagged on July 4 at 150° W, reached the Nass River area on July 31 (distance about 700 miles). Bristol Bay sockeyes have shown a rather definite eastward limit of distribution in the Gulf of Alaska, from April onward, at about 143–145° W long (Margolis, 1963; Neave *et al.*, MS, 1963). A fish tagged at 145° W, on June 2, 1962, was recovered in Bristol Bay 35 days later (distance about 900 miles).

fish. Presumably, therefore, a lengthy coastward journey may be made more than once during the ocean life of this species. Both pinks and chums continue to feed and grow throughout the migrations, which permit the exploitation of additional ocean areas.

From this viewpoint the return of salmon from distant ocean localities is not necessarily wholly a "spawning migration" but rather a journey or journeys which permit the fish to make the best use of the marine environment. For pink salmon spawning in the rivers of the northwestern Gulf of Alaska and the Karagin coast of Asia it seems likely that seasonal changes in the environment would favour a fairly direct route from the spring feeding areas to the spawning streams. Tagging results lend support to this view. However, since the fish of a given stock in spring are scattered over a wide region the direction taken by individuals varies widely, as has been noted.

THE OCEAN MIGRATIONS OF IMMATURE SALMON

In British Columbia, pink and chum salmon fry commonly enter the sea in April and May and can be seen in large numbers along shorelines for some weeks thereafter. About July they disappear from the water's edge but some can still be caught in strictly coastal waters until autumn. A trawl catch of 163 juvenile pinks and 69 juvenile chums was made in Dixon Entrance on November 5, 1963. On the Asian side numbers of young pinks have been reported in the inshore waters of the Maritime Province and the west coast of Sakhalin Island as late as October and November (Pravdin, 1940; Dvinin, 1952). Young sockeyes which had entered the sea in spring (after spending a year or more in fresh water) have been taken among the islands of the central British Columbia coast until September. On the other hand young pink salmon (of unknown origin) have been encountered at distances of up to nearly 100 miles offshore in the Gulf of Alaska in late August and September (Hartt, 1962).

The courses followed by young salmon during the months immediately following their evacuation of coastal waters are not known. However, spring fishing operations on the high seas have shown that at least some of these small fish make very extensive journeys during this period. Pink salmon tagged in April 1962 were 800–1100 miles southeast of the central Alaskan localities to which they subsequently migrated (Fig. 6). Assuming they had left the same coastal localities in the previous July, they would have required an average travel rate of 3–5 miles a day on a direct course, to reach the tagging points in the available period of about 9 months. In 1963, four pink salmon were recovered off the Karagin coast which had been tagged in the western Gulf of Alaska in May of that year (Fig. 6). At that time these fish were 1500 or 1600 miles from their destination and on a similar calculation must have travelled at a minimum average speed of about 5 miles per day on the outward journey. That the fish cited in these examples were not aberrant individuals is clearly indicated by consideration of other tagged pink salmon which returned to these same coastal areas. The total ocean area occupied by each coastal "stock", although large, is cohesive and the early-season positions of fish at distant places

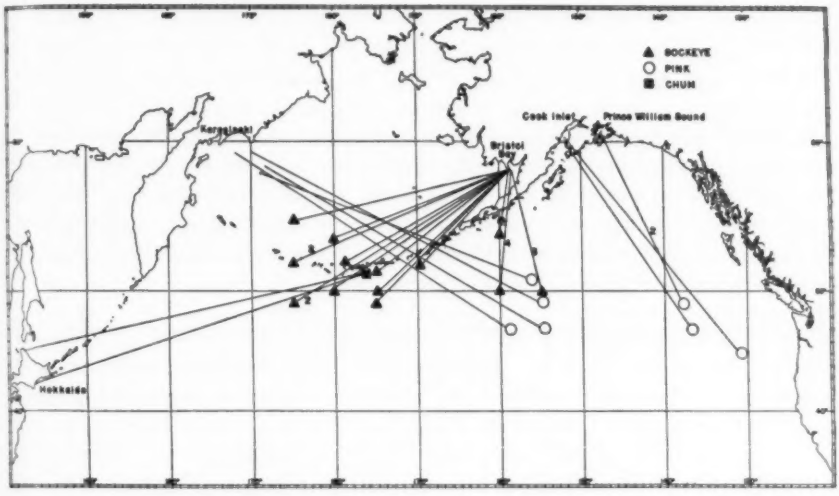


FIG. 6. Positions occupied by young salmon, associated with various areas, after one winter in the ocean.

are supported by many recoveries of fish tagged at later dates at points between these places and the breeding areas.

Sockeyes bearing the cestode characteristic of Bristol Bay stocks (*Triaenophorus crassus*) have been caught after about a year of ocean life eastward to 155°W and westward to 175°E (Margolis, 1963) as shown in Fig. 6. The distances from Bristol Bay, by sea, are about 550 to 1100 miles, implying minimum travel rates of 1½–3 miles per day.

Chum salmon tagged near Adak Island in June and July 1956, after one winter in the ocean, were recovered in later years from northwest and east Hokkaido (Hartt, 1962). These positions are also shown in Fig. 6. The distance between tagging and recovery areas is about 1600 miles and if these fish left the latter areas a year prior to their capture on the high seas their minimum rate of eastward progress must have been more than 4 miles per day.

These examples suggest that young salmon after leaving inshore waters often make net progress in consistent directions over long distances and time-periods. In general, the minimum rates of travel given above are not dissimilar from those recorded by Johnson and Groot (1963) for sockeye smolts migrating through Babine Lake in the early stages of their seaward journey. These investigators reported mean rates of about 3–6 miles per day over courses of from 27 to 63 miles. With increasing size during their ocean life a higher rate of travel could no doubt be maintained. On the other hand the rates indicated for high-seas travel could be much too low. The routes taken may well conform with a variety of external conditions imposing a longer distance. Also, it is not known how long the fish had been at the tagging areas before being caught — or whether, indeed, they were not already part way on the return journey.

CURRENTS IN RELATION TO OCEAN MIGRATIONS

Obviously currents must affect the direction, speed, or effort involved in travelling over long ocean distances. The possibility that much migration is accomplished essentially by passive drifting is examined briefly.

The features of the sub-Arctic Pacific circulation are described by Dodimead *et al.* (1963). They include four gyres: Bering Sea, western sub-Arctic, Okhotsk Sea, and Alaskan (see Fig. 7). Most of the Pacific salmon reaching offshore waters would be subjected to currents associated with one or more of these gyres. However, the idea that salmon return to their spawning areas by drifting is clearly untenable, for the following reasons.

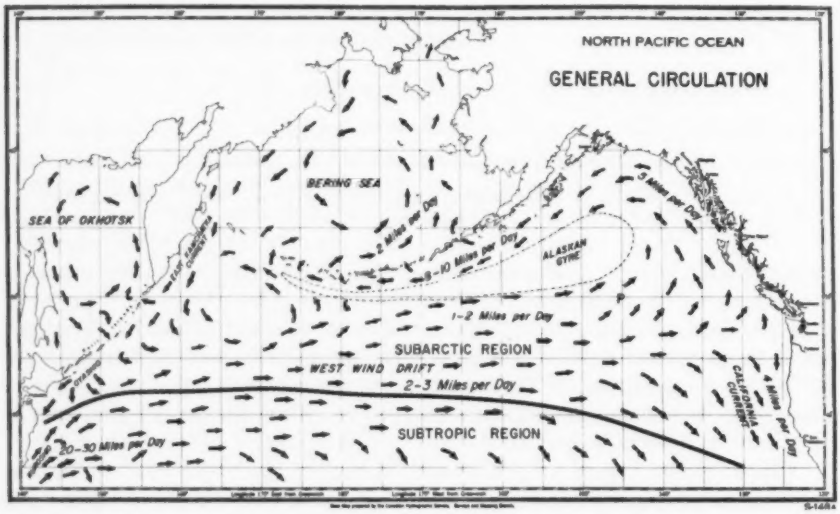


FIG. 7. General circulation of surface water in the North Pacific Ocean and adjacent seas (by A. J. Dodimead).

1. No drift pattern can be imagined which, unaided, could conduct salmon, starting from many widely separated coastal areas, on round trips terminating at the starting points at a precise season and stage of maturity. Moreover, many salmon entering the sea at the same time from the same river system mature and return at different ages[4].

2. The considerable degree of geographical segregation of species in the high seas could hardly be effected by passive drift.

[4]For example, sockeye salmon of the Skeena River and of Rivers Inlet, B.C., return in large numbers both as fourth-year and as fifth-year fish. The return from a given brood-year may consist of approximately equal numbers in each of these categories or may show varying degrees of preponderance of either age-group. A few fish (about 1–5% of the total return) are in their sixth year (Godfrey, 1958; Shepard and Withler, 1958). The pink salmon which leave these river systems at nearly the same time of year as the sockeyes, of course return at 2 years of age. Marked chum salmon fry, released in Hooknose Creek, B.C., returned as third, fourth, and fifth-year fish in percentages of 19.7, 71.8, and 8.5, respectively (Hunter, 1959).

3. Fish of the same ocean age from many widely separated places of origin are often found in the same high-seas area at the same time, and, as we have seen, maturing fish proceed simultaneously in many directions from a common high-seas position.

4. In the course of their ocean life many fish are associated with more than one of the gyral systems, e.g. the Karagin pink salmon which penetrate into the region of the Alaskan gyre.

5. The velocity and direction of recorded currents are often entirely inadequate to account for the rate of travel. In the central and eastern parts of the Gulf of Alaska, where current velocities are commonly of the order of 1–4 miles per day, the minimum travel speeds of tagged sockeye and pink salmon over distances of several or many hundred miles has frequently exceeded 25 and sometimes 40 miles per day. Moreover, these journeys were made in a wide variety of directions relative to the known currents. Hartt (1962) found that sockeyes returning to Bristol Bay through the eastern Bering Sea (an area of weak, northward-flowing currents) averaged about 30 miles per day.

From data presented previously in this paper, it is evident that freedom from the limitations of speed and direction dictated by currents extends also to the outward migrations of juvenile salmon. The distant positions occupied by young salmon within a year of their departure from coastal localities could not have been reached within this time-period by any reasonable interpretation of the velocity and direction of known currents. It can be stated with considerable confidence that to drift from the Karagin coast or Prince William Sound to the areas far to the southeast to which the pink salmon of these regions penetrate, would require a much longer period than the total ocean life-history of the species—without any consideration of the necessity for a return journey. Even the Hokkaido chums, whose eastward progress toward the central Aleutians could well be facilitated by use of the sub-Arctic current, might be expected to take about twice as long as the evidence indicates they actually took. It seems that the young Bristol Bay sockeyes which appeared in the western part of the Gulf of Alaska after one winter in the ocean must have resisted northward-flowing currents in the Bering Sea and in the passages of the Aleutians and then overcome the tendency of the strong Alaskan stream to carry them far to the west.

It is concluded that salmon are able to reach distant ocean areas which offer favourable conditions for survival and growth, and also to return from these areas, by relatively rapid journeys which are not closely controlled by currents.

VIEWS ON CLUES

On the basis of the kinds of evidence mentioned previously, speculation on the means whereby salmon direct their ocean migrations must take account of the following conclusions: (a) Salmon can reach preferred distant feeding areas and can return to precise coastal localities without relying on transportation by currents. (b) Salmon "starting" from a common point on the high seas can maintain widely divergent courses over long distances toward their respective

widely separated places of origin. (c) Salmon from widely separated high-seas localities can converge on a coastal locality, arriving at the latter with a high degree of precision in timing.

The view has sometimes been expressed (verbally, if not in published literature) that the high-seas journeys of returning salmon need only be directed with sufficient accuracy to reach some part of a major coastline which can then be SEARCHED until local clues, such as landmarks or odours, indicate the vicinity of the home stream. There are serious objections to this view. From some of the feeding grounds occupied by maturing salmon a deviation of only a few degrees in direction could result in the fish approaching the "wrong" continent (Asia or North America, as the case might be). Even without this eventuality a "blind" landfall could be expected to necessitate coastal journeys varying from insignificant distances to many hundreds of miles — presumably with no indication of the time necessary to reach the destination. If there was an inherited tendency to turn in one direction, say, right rather than left on reaching a coastline, the usefulness of such a tendency would depend largely on the accuracy of the previous course in aiming to the left of the target. It has been mentioned that some runs of salmon make extensive journeys in coastal waters. These journeys, however, give the impression of concerted, well-timed migrations in a consistent direction rather than a search for clues by individuals which have "landed" haphazardly along a vast coastline. It is indeed hard to believe that a coastline such as that of British Columbia and southeast Alaska would provide a useful guide to an erring salmon. Strict adherence to a shoreline would inevitably condemn the migrant to continual circling of one of the numerous islands which fringe these coasts. To advance effectively it would be necessary to *leave* a shoreline at appropriate points.

The view that CURRENTS might provide guiding clues (even if they do not furnish actual transportation) fails to explain how orientation to a current can be effected in the absence of fixed reference points. If orientation *could* be effected it would still be necessary to explain how the fish could determine the places or times at which changes in orientation would be needed to maintain an appropriate direction of travel. It has already been noted that travel rates are commonly much greater than known current velocities.

It is accepted that each species of salmon has a preferred range of TEMPERATURE. Reference has been made to seasonal movements which correspond with temperature changes and to the likelihood that in some instances the route followed by maturing fish may be influenced by unfavourably warm water. However, it does not seem possible to hold the view that salmon could direct themselves to a particular coastal area by following a TEMPERATURE GRADIENT. At the season when the maturing sockeyes begin their shoreward migrations from their feeding grounds in the middle of the Gulf of Alaska (May to July) the waters due north of them show little or no temperature gradient, the waters east of them are warmer, and the waters westward are slightly cooler. Yet the fish migrate in large numbers in all these directions. Actually the steepest gradient is to the south — the worst possible direction for a shore-seeking fish.

SALINITY differences in the open-ocean regions occupied by salmon are very slight and irregular. The sockeye feeding area mentioned above coincides more or less with the highest salinities in the Gulf of Alaska. Slight gradients therefore exist in most directions. The total change in salinity that might be experienced by a salmon proceeding from the feeding area toward the Fraser River would be of the order of 0.6‰ or 0.8‰ over the first 700 miles of travel — or an average of 0.01‰ over a 10-mile distance.

Apart from the lack of evidence that salmon are able to follow the kinds of gradients (of temperature, salinity, or other chemical nature) which occur in the ocean, it does not seem possible that these could provide directional clues sufficiently precise to be useful either in establishing an initial orientation or in maintaining a course.

From the speed with which salmon cover long distances it seems evident that whatever directional clues are used do not necessitate long periods of random searching or frequent major "corrections".

It is reasonable to suppose that the time actually used by the fish for active migration is considerably less than the number of days spent. Johnson and Groot (1963) found indications that sockeye smolts in Babine Lake migrated actively during about 6½–8½ hr of the 24-hr day and that much time was spent in feeding. The proportion of the day that is spent in active migration by maturing salmon in the ocean is not known. However, the readiness with which these fish are caught by baited hooks and the evidence provided by examination of many stomachs show that extensive feeding takes place during the period of migration. LeBrasseur and Parker (1964) found that growth of pink salmon continued until the fish were close to their freshwater destinations. An 8-hr migrating day would demand sustained travel speeds of 3–3½ mph, in a direct line, to account for such commonly observed performances as a daily net progress of 25–30 miles per day — maintained over periods of many days.

The ability of certain freshwater fishes to set and maintain a course using the sun as reference was demonstrated by Hasler *et al.* (1958). ORIENTATION BY CELESTIAL FEATURES by young sockeye salmon in fresh water was found by Johnson and Groot (1963). These investigators also reported that the direction of orientation changed over a period of about 2 weeks in the case of a population of fish whose attainment of the outlet of a lake demanded a similar change of direction during the course of their migration. The inference is that each stock can set a course or courses appropriate to the rapid performance of a normal migration through genetically determined responses. This "implies the existence of an internal clock or diurnal rhythmic sense that allows the fish to make the proper adjustments to the diurnally and seasonally changing phenomena".

There is no reason to doubt that the orienting ability possessed by young salmon is retained in the later ocean-dwelling stages of the life-history, when the need and scope for such ability would seem to be much greater. There are difficulties, however, in supposing that this ability alone is sufficient to account for the apparent precision with which salmon return to small coastal areas. An

initial point for consideration is the prevalence of cloud-cover throughout the high-seas regions occupied by salmon. In most of these regions, in summer, an "average" condition is represented by a 70–80% obscuration of the sky (Dodimead *et al.*, 1963). While this statistic does not reveal the frequency or magnitude of breaks in the cloud-cover it is the experience of investigators that there are many days when the sun cannot be seen at any time. The opportunities for observing fainter celestial features, such as stars or night-sky patterns, would naturally be fewer still.

While it has been shown that certain crustaceans and other invertebrates can orient with respect to *polarized light* (e.g. Waterman, 1959), there seems to be no published information on the ability or otherwise of salmon to use this feature of the environment as a directive guide. The viewing of any celestial features by salmon would of course depend on their presence sufficiently close to the surface and on their powers of vision. In this connection it can be stated that fishing experience has shown that many, perhaps most, salmon are very close to the surface at about the time of sunrise. Some salmon are also at the surface at other times of day but daytime catches of sockeyes and chums have been made in waters as deep as 160–200 ft (Anon., 1961).

Another, perhaps more serious, difficulty lies in understanding how a useful compass direction toward a small coastal area could be established without some information on the position from which the course is taken — that is, in human terms, a knowledge of latitude and longitude relative to the place of origin. Johnson and Groot concluded that for their sockeye smolts in the relatively restricted environment of a lake "the complicated route of the . . . smolts can be sufficiently explained by shifting one-directional (celestial?) orientation and does not imply bico-ordinate navigation". In the ocean, however, if the direction taken is merely a genetically determined tendency to orient, say, northwest when a certain stage of maturity is reached, how is allowance made for drifting or other movements which have taken place during the 1, 2, or 3 years previously spent in the ocean? From evidence cited previously it can be concluded that salmon actually return expeditiously to a particular area from various directions representing quite different compass courses many of which would be quite inappropriate if the positions of different fish were interchanged. For example, if the westernmost fish shown in Fig. 5 had followed a compass course in accordance with the direction of net progress of the easternmost fish they would have eventually reached the Aleutian Islands or even the Asian coast instead of Kodiak Island.

It is difficult to avoid the conclusion that throughout the period of ocean life some awareness of position in relation to the place of origin is maintained. If this is so, such information must have been available (continually or by means of a series of "observations") from the time when the animal entered the ocean. The "clock" required for such observations would have to be capable not only of telling the local time of day but also of comparing local time with "home" time throughout changing seasons.

While suggestions regarding such a mechanism are as yet purely speculative it can be mentioned that there is evidence that salmon, from the earliest stage of free-swimming life, have a keen appreciation of changes in light intensity and length of day. Pink, chum, and sockeye salmon emerge from the gravel and migrate downstream only when the light intensity falls to a certain very low level at night. Artificial light was found to prevent sockeye fry from beginning their nightly migration at the usual time. However, when the artificial light was removed, after delaying migration for 2 or 3 hr, migration was initiated more abruptly than under natural conditions (McDonald, 1960). This suggests that although the fish waited for appropriate external conditions an internal clock informed them of the delay.

In the ocean, appreciation of length of day and of local time may be reinforced by feeding habits. Most, if not all, of the organisms on which salmon feed show extensive diel vertical migrations. It may be supposed that evening and morning bring a succession of organisms, responding to different light intensities, into or through the level occupied by salmon.

A change in latitude might be registered as a change in length of the period of darkness; a change in longitude as a change in the time at which darkness begins and ends. The compass course taken (using the sun or other celestial feature as a reference) might depend on this kind of information. The comment of Matthews (1955) on bird navigation is appropriate: ". . . the ability is so extraordinary that the solution of the problem can hardly fail to be extraordinary in itself. All suggestions therefore deserve a close scrutiny before they are rejected".

Whatever the abilities and clues involved may be, suggestions regarding the mechanism of ocean migrations should not confine themselves to the final homing journey. The ocean life of salmon is an integrated whole, involving the passage of the young fish to appropriate areas and seasonal movements (or resistance to movement) whereby the animals exploit the environment during the many months prior to their return to fresh water.

ACKNOWLEDGMENTS

Many of my associates at the Nanaimo Station took part in procuring data which have been used in this paper. Mr A. J. Dodimead kindly supplied the figure showing water circulation in the North Pacific. Dr P. A. Larkin helpfully reviewed the manuscript.

REFERENCES

ANON. 1961. International North Pacific Fisheries Commission, Annual Report for 1960.

1964. International North Pacific Fisheries Commission, Annual Report for 1962.

CLEMENS, W. A. 1951. On the migration of Pacific salmon. *Proc. Roy. Soc. Canada*, 45, ser. 3, sect. V, 9–17.

DODIMEAD, A. J., F. FAVORITE AND T. HIRANO. 1963. Review of oceanography of the sub-Arctic Pacific region. *Bull. International North Pacific Fisheries Commission*, No. 13, 195 pp.

DVININ, P. A. 1952. [The salmon of South Sakhalin]. *Izvestiia Tikhookeanskovo Nauchno-issledovatelskovo Instituta Rybnovo Khoziaistva i Okeanografii*, **37**: 69–108. [FRBC Translation Series No. 120.]

GODFREY, H. 1958. A comparison of sockeye salmon catches at Rivers Inlet and Skeena River, B.C., with particular reference to age at maturity. *J. Fish. Res. Bd. Canada*, **15**(3): 331–354.

HARTT, ALLAN C. 1962. Movement of salmon in the North Pacific Ocean and Bering Sea as determined by tagging, 1956–1958. *Bull. International North Pacific Fisheries Commission*, No. 6, 157 pp.

HASLER, A. D., R. M. HORRALL, W. J. WISBY AND W. BRAEMER. 1958. Sun-orientation and homing in fishes. *Limnol. and Oceanogr.*, **3**(4): 353–361.

HUNTER, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. *J. Fish. Res. Bd. Canada*, **16**(6): 835–886.

JOHNSON, W. E., AND C. GROOT. 1963. Observations on the migration of young sockeye salmon (*Oncorhynchus nerka*) through a large, complex lake system. *J. Fish. Res. Bd. Canada*, **20**(4): 919–938.

LEBRASSEUR, R. J., AND R. R. PARKER. 1964. Growth rate of central British Columbia pink salmon (*Oncorhynchus gorbuscha*). *J. Fish. Res. Bd. Canada*, **21**(5): 1101–1128.

MANZER, J. I., T. ISHIDA, A. E. PETERSON AND M. G. HANAVAN. MS, 1963. Offshore distribution of salmon. Int. North Pac. Fish. Comm., Vancouver, B.C.

MARGOLIS, L. 1963. Parasites as indicators of the geographical origin of sockeye salmon, *Oncorhynchus nerka* (Walbaum), occurring in the North Pacific Ocean and adjacent seas. *Bull. International North Pacific Fisheries Commission*, No. 11, pp. 101–156.

MATTHEWS, G. V. T. 1955. Bird navigation. Cambridge University Press. 141 pp.

MCDONALD, J. 1960. The behaviour of Pacific salmon fry during their downstream migration to freshwater and saltwater nursery areas. *J. Fish. Res. Bd. Canada*, **17**(5): 655–676.

NEAVE, FERRIS, AND M. G. HANAVAN. 1960. Seasonal distribution of some epipelagic fishes in the Gulf of Alaska region. *J. Fish. Res. Bd. Canada*, **17**(2): 221–233.

NEAVE, F., J. I. MANZER, H. GODFREY AND R. J. LEBRASSEUR. MS, 1963. High-seas salmon fishing by Canadian vessels in 1962. *Fish. Res. Bd. Canada MS Rept. (Biol.)*, No. 759, 59 pp.

PRAVDIN, I. F. 1940. [A review of investigations on the far-eastern salmons.] *Izvestiia Tikhookeanskovo Nauchno-issledovatelskovo Instituta Rybnovo Khoziaistva i Okeanografii*, **18**: 5–105. [FRBC Translation Series No. 371.]

SAILA, SAUL B., AND RAYMOND A. SHAPPY. 1963. Random movement and orientation in salmon migration. *J. du Conseil*, **28**(1): 153–166.

SHEPARD, M. P., AND F. C. WITHLER. 1958. Spawning stock size and resultant production for Skeena sockeye. *J. Fish. Res. Bd. Canada*, **15**(5): 1007–1025.

WATERMAN, TALBOT H. 1959. Animal navigation in the sea. *Gunma J. Med. Sci.*, **8**(3): 243–262.

A Model for Simulation of the Population Biology of Pacific Salmon[1]

By P. A. Larkin and A. S. Hourston

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

A model simulating the population dynamics of the stocks of salmon spawning in a large river system is constructed, incorporating (1) a series of theoretical reproduction curves operating in successive stages during the life history of each stock producing compensatory or depensatory effects, (2) a device for simulating environmental variability (extrapensatory effects), (3) the effects of a joint fishery on mixed stocks, (4) the effects of multiple age of spawning on fluctuation in abundance of a single stock, (5) the consequences to yield of various degrees of stabilization of the fishery, and (6) the inheritance of age at maturity in salmon. Application of the model is illustrated by two examples. The first simulates the production of cyclic dominance by the inheritance of age of maturity and depensation in the freshwater stage. In the second example, five stocks differing in relative abundance, age composition, environmental variability, and rate of compensation are subjected to a common fishery which is selective for age and provides for complete stabilization of the escapement for the combined run as a whole. Comparisons between various combinations of the five stocks show the effects of these factors on the various stocks and on the run as a whole over a simulated period of 120 years.

INTRODUCTION

Ricker (1954) developed the concept of reproduction curves for description of the relation between stock and recruitment for a single population of fish, using the compensatory process depicted by the formula

$$Z = We^{a_1(1-W)} \qquad (1)$$

Also considered were the effects of multiple age of spawning on the pattern of fluctuation in a single stock, and a device for simulation of environmental variability. In a later paper, Ricker (1958) described the effects of a joint fishery on mixed stocks and the consequences to yield of various degrees of stabilization of escapement.

All of these features may be combined in a model for simulation of the population dynamics of the stocks of salmon spawning in a large river system. Empirically, one can then study the properties of mixed stocks, each subject to its own environmental variability and jointly harvested by a fishery which might operate in any of a variety of ways. It is with such a simulation that this paper is concerned.

Two further features of salmon population biology seem worthy of inclusion in a general approach to the problem of simulation. Larkin *et al.* (1964) suggested various alternative premises in the construction of theoretical reproduction

[1]Received for publication June 8, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

curves, and particularly pointed out the possibilities of considering sequences of "reproduction curves" for various life-history stages, the output from one stage comprising the input for the next. Ward and Larkin (1964) used such a sequence in a model for simulation of the phenomenon of cyclic dominance in sockeye salmon of the Adams River race. In a model for simulation of population events in a complex river system it seems appropriate to provide for a variety of life-history stages for each population, and not necessarily the same sequences for the various populations.

The second consideration concerns the inheritance of age at maturity in salmon. Ricker's (1954) considerations for multiple-age spawning stocks were based on the assumption of fixed age composition, i.e. the recruitment age composition was not influenced by the stock age composition. The correlations and deductions of Godfrey (1958) suggest for some British Columbia sockeye stocks, that inheritance plays at least some part in determining age composition of a brood. Accordingly, a model for simulation should provide for recruitment influenced by stock age composition.

In view of the complexity of a model which incorporates the foregoing, the use of a computer for empirical calculations is almost obligatory. The structure of the model is described and some examples of its application are given in subsequent sections. Copies of the computer program (Fortran II) are on file at the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.

GENERAL PLAN OF THE MODEL

The general plan of the model for simulation of a salmon run is diagrammed in Fig. 1 and summarized algebraically in Table I. In the marine stage, all stocks are considered to share a common environment and the run is shown as a unit (large boxes in Fig. 1). At the beginning of the first simulated year, a

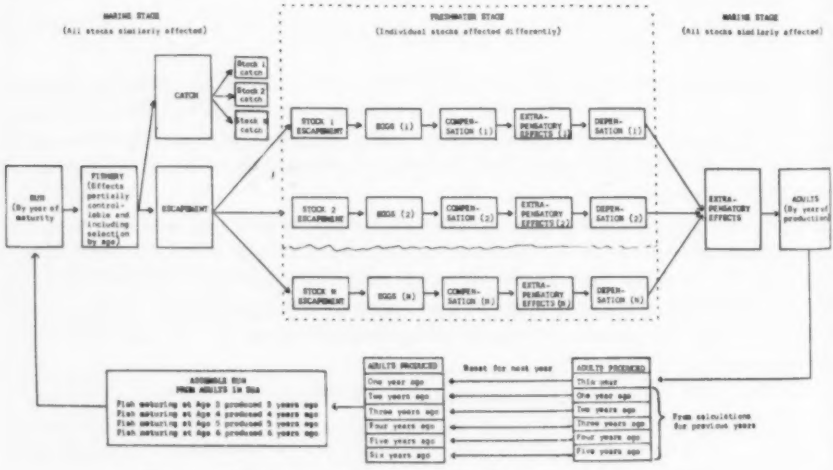


FIG. 1. Diagram showing stages included in model of salmon run.

run is assembled consisting of those fish of various brood years which are to become mature, i.e. the fish produced 3 years ago which mature at age 3, the fish produced 4 years ago which mature at age 4, and so on. This run is then subjected to a fishery on the run as a whole, in which the rate of removal and/or the escapement can be regulated. In addition the fishery may be arranged as to be more effective (selective) at catching fish of a certain size (age). The allowable catch is distributed first among the various ages and is then subdivided amongst the various stocks. The escapements by ages for the various stocks are obtained by subtracting the catches from the original contributions of the various groups to the total run.

In the freshwater stage, each stock has a unique environment, and the stocks are treated separately (small boxes in Fig. 1).

The proportions of each brood which will subsequently mature at each age are estimated from the proportions of each age group in the spawning population. The egg deposition is then calculated for each stock. Next, it is assumed that this new brood of young fish is subjected to mortalities which are in turn compensatory (increasing percentage with increasing abundance), extrapensatory (fortuitous), and depensatory (decreasing percentage with increasing abundance), and which are related to the environmental conditions the simulated stock encounters. The order of operation and intensity of these effects may be varied according to the environmental conditions visualized for the stock being simulated.

The new broods from each stock then proceed to the "sea" where they are considered to share a common environment and the run is shown as a unit (large boxes in Fig. 1). Here they encounter a further set of extrapensatory effects. Compensatory and depensatory effects during the marine stage are not considered in the present model although they could be provided if desired.

In subsequent appropriate years, portions of the productions from each of the stocks are reassembled to comprise spawning runs for particular calendar years.

The model deals exclusively in *stock units*, so that at equilibrium one unit of egg deposition produces one unit of fry, and so on throughout the various life-history stages. Age composition is also stable at equilibrium because age at maturity of a brood is related to age at maturity of the spawners which produced it. Similarly, egg production is related to age composition so that the initial equilibrium is stable in the absence of a fishery.

DESCRIPTION OF THE MODEL

The Run and the Fishery

A *run* in a particular calendar year comprises individuals of various ages produced by various brood years, for each of *k stocks*. At equilibrium the various stocks may be visualized as being of differing magnitudes of size. Thus a stock unit for the population of a large lake or stream may represent ten times the number of individuals as a stock unit for a smaller system. Accordingly, in the construction of the run each stock is multiplied by a factor indicating its *magnitude*.

TABLE I. Chronology of computations for each brood year in model simulating a salmon run.

Stage	Equation	Equa. No.	Legend
Adult run reconstruction	$A_{ik} = N_{jk} \cdot Pmat_{ijk}$	2	A_{ik} = numbers of adults in stock units of ages i in stocks k in the run for a calendar year
	$T_{ik} = A_{ik} \cdot V_k$ $T = \sum_{ik} T_{ik}$	3	N_{jk} = numbers of adults in stock units of all ages produced by the brood year j years ago for each stock k $Pmat_{ijk}$ = proportions of adults of ages i produced by the brood years j years ago in stocks k, note $i = j$ V_k = relative orders of magnitude of various stocks k T_{ik} = numbers of adults of ages i adjusted for orders of magnitude of various stocks k T = total number of adults in the run
Catch	$P_{ik} = T_{ik} \cdot S_i \cdot F$	4	P_{ik} = proportional catches of fish of ages i from stocks k S_i = selective rates of harvesting of fish of ages i F = rate of fishing for the run
	$C_{ik} = \frac{P_{ik}}{\sum_{ik} P_{ik}} \cdot \frac{H}{V_k}$	5	C_{ik} = catches of fish in stock units of ages i from stocks k H = permissible harvest
Escapement	$E_{ik} = A_{ik} - C_{ik}$	6	E_{ik} = escapement in stock units of fish of ages i of stocks k
Proportion at maturity (for each stock k)	$E_{i-3} = E_{i-3} \cdot J$		E_{i-3} = escapement of jacks J = jack factor
	$Pmat_i = \frac{E_i}{\sum_i E_i}$	7	$Pmat_i$ = proportion of progeny which will mature at ages i in various j years hence, note $i = j$ E_i = escapements of fish of ages i
Egg production (for each stock k)	$W = \sum E_i \cdot G_i$	8	W = egg production in stock units G_i = egg production factors for ages i
Fry production Compensatory mortality (for each stock k)	$Z = We^{a_1(1-W)}$ $Z = (1 - D)e^{-a_2(W-1)} + D$ (optional for $W > 1$)	1 9	Z = potential production of fry a_1 = compensation coefficient for egg to fry stage a_2 = saturation coefficient D = compensation asymptote

TABLE I.—Continued

Stage	Equation	Equa. No.	Legend
Extrapensatory mortality (for each stock k)	$\begin{cases} R = Z \cdot (\lvert RND \rvert \cdot Q_1 + 1), RND + \\ R = Z / (\lvert RND \rvert \cdot Q_1 + 1), RND - \end{cases}$	10	R = actual fry production RND = random normal deviate $Q_{1,2}$ = scaling coefficients for determining ratio of extreme effects
Smolt production (for each stock k)			
Compensatory mortality	$M = Re^{a_s(1-R)}$	1	M = smolt production a_s = coefficient of depensation (or compensation)
or			
Depensatory mortality	$M = Re^{a_s(R-1)}$, $R<1$ $M = R$, $R>1$	11	
	where a_s = constant		
	or		
	$a_s = F'_1 \cdot R_{t-1} + F'_2 \cdot R_{t-2} + F'_3 \cdot R_{t-3}$	12	F'_1, F'_2, F'_3 = coefficients relating fry production in previous years to rate of depensation
	or		
	$a_s = F_1 \cdot W_{t-1} + F_2 \cdot W_{t-2} + F_3 \cdot W_{t-3}$	12	F_1, F_2, F_3 = coefficients relating egg production in previous years to rate of depensation
or			
Smolt buffered depensation	$B = R + S_B \cdot M_{(t-1)}$	13	B = provisional smolt production
	$M = Re^{a_s(B-1)}$, $B<1$	14	S_B = coefficient relating smolt biomass to fry biomass
or	$M = R$, $B>1$		$M_{(t-1)}$ = smolt production for previous brood
No compensation or depensation	$M = R$		
Adult production	$\begin{cases} N_k = M_k (\lvert RND \rvert \cdot Q_2 + 1), RND + \\ N_k = M_k / (\lvert RND \rvert \cdot Q_2 + 1), RND - \end{cases}$	10	

Thus $$A_{ik} = N_{jk} \cdot Pmat_{ijk} \quad (2)$$

where A_{ik} are the numbers of adults in stock units of ages i, in stocks k in the run for a calendar year

N_{jk} are the numbers of adults in stock units of all ages produced by the brood year j years ago for each stock k

$Pmat_{ijk}$ are the proportions of adults of ages i produced by the brood years j years ago in stocks k, note $i = j$.

The summation of the assembled run (T) of a particular year is given by,

$$T_{ik} = A_{ik} \cdot V_k$$

$$T = \sum_{ik} T_{ik} \quad (3)$$

where V_k are the relative sizes of the stocks

T_{ik} are the numbers of adults of ages i adjusted for orders of magnitude of various stocks k.

From this assembled run, the 3-year-olds ("jacks") are then subtracted, because in practice they are ignored in the decision making procedure in the fishery. The remainder, called the *fishable run*, is then processed through a *fishery* which may harvest the run as a whole in one of several ways (Ricker, 1958):

(1) fixed percentage exploitation;

(2) partial stabilization of escapement — harvesting the surplus over a fixed (usually the optimum) escapement but not to exceed a fixed percentage exploitation; and

(3) complete stabilization of escapement — harvesting the surplus over a fixed (usually the optimum) escapement.

For each of these procedures, the permissible harvest is divided by the fishable run, to provide a *fishing rate*, to be applied to the fishable run, or, if desired, to the whole run, i.e. including the "jacks". Because various ages may be differentially exploited, provision is made for inclusion of factors of *selectivity*, thus requiring in the procedure a proportional allocation of catch.

The proportional catch (P) of a particular age (i) of fish from a particular stock (k) is given by

$$P_{ik} = T_{ik} \cdot S_i \cdot F \quad (4)$$

where T_{ik} are the numbers of maturing adults of ages i and stocks k

S_i are the selective rates of harvesting of fish of ages i

F is the rate of fishing for the run.

The permissible harvest can then be assigned to the various ages in the various stocks in proportion to their contribution to the total proportional catch.

Catches by stocks can then be converted to stock units by dividing by the magnitude factors.

Symbolically,

$$C_{ik} = \frac{P_{ik}}{\sum_{ik} P_{ik}} \cdot \frac{H}{V_k} \tag{5}$$

where C_{ik} are the catches in stock units of fish of ages i from stocks k

H is the permissible harvest.

Escapements, as the basis for production in separate stocks, must be expressed in stock units. They are therefore calculated as the residues after catches in stock units are subtracted from the adults in stock units for each age and each stock in the run, i.e.

$$E_{ik} = A_{ik} - C_{ik} \tag{6}$$

where E_{ik} are the escapements in stock units of fish of ages i of stocks k.

Inheritance of Age Composition

At first glance it would seem reasonable to relate the age composition produced by a brood to the relative contribution the various ages made to the egg production of the escapement. For two reasons this procedure would be inadequate. First, it would take no account of the contribution made by male fish in determining age at maturity of progeny of a particular spawning. For instance, it would imply that there was no genetic machinery involved in the production of jacks, which are almost exclusively males. If egg production contributions were the only consideration, the simulation would eliminate jacks from the population within a very few generations, contrary to what is observed in nature. Similarly, because older ages produce more eggs they would progressively constitute a greater proportion of the population. Thus, the second reason for not using egg production contributions for determining age composition of the progeny at maturity, is that they take no account of the additional mortality experienced by the older fish, in the course of the greater number of years expended from one generation to the next.

These difficulties can be circumvented if it is assumed that by natural selection, the age composition of a stock would achieve stability in the absence of a fishery. This stability would reflect, among other factors, that on the average the greater fecundity of older fish compensated their lesser survival to maturity. On this assumption it is appropriate to relate age composition of the progeny of a brood to age composition of the parent escapement. This procedure is followed in the model for each stock (k), the proportion of the progeny maturing at a particular age (Pmat_i) being the proportion which that age contributed to the adult escapement, viz.

$$\text{Pmat}_i = \frac{E_i}{\sum_i E_i} \tag{7}$$

One important modification must be made to this procedure, again because of the peculiarities of the jacks. Being almost exclusively males, their effect on age composition is determined by their participation in the spawning act with older females. The extent of this participation is probably not directly in proportion to their abundance relative to other ages of male fish (perhaps, because they are smaller, they are less successful in competition for mates). In the natural situation it is possible also that the proportion of jacks resulting from a brood is in large part determined environmentally. In any event, the procedure of equation (7) would only maintain a stable proportion of jacks in the absence of a fishery. With a substantial fishery only on the other ages, the jacks would soon swamp the population, so that it comprised a very large number of individuals of very low fecundity, contributing nothing to the harvest. To a degree this may indeed occur, but not to the extent implied by the procedure of equation (7). Thus, in the model, to approximately weight the contribution made by jacks in determining the age composition of a brood, the escapement of jacks was multiplied by a *jack factor* before it was included in the summation of equation (5). The value of this jack factor defines the rate at which jacks will form an increasing proportion of a stock exposed to a fishery which does not harvest jacks. If, for example, the jack factor is set equal to (1–F), the effect is to reduce the contribution of the jacks to the same extent as the older ages are reduced by the fishery and hence to keep the age composition constant.

Egg Production

The escapement for each stock consists of various ages of fish which make differing contributions to the egg deposition. Fish which mature at older ages produce more eggs per individual. In addition, males preponderate at the younger ages. Each age group is therefore corrected by an *egg production factor* in the calculation of the *stock of eggs*. An important restraint is that at equilibrium at one stock unit, the stock of eggs must equal one stock unit. Thus the sum of the products of the escapements of fish of a particular age and the relative numbers of eggs these fish produce must equal one. Thus, for any stock (k), at equilibrium,

$$\Sigma E_i G_i = W = 1 \qquad (8)$$

where E_i are the escapements in stock units of fish of various ages (i)

G_i are the egg production factors which take account of number of eggs per fish and the sex ratio of fish of various ages

W is the egg production in stock units.

Compensatory Stage of Mortality

Some stage of a simulated life history of a population must be compensatory if the population is to be neither increasing nor decreasing indefinitely. Although several successive stages of compensation could be envisaged (Larkin *et al.*, 1964), for salmon as a whole it seems reasonable to assume that compensation occurs

chiefly in the first stages of production of a brood — amongst the adults as they compete for a spawning site or amongst the eggs as they "compete" for oxygen in the gravel. Losses occasioned by the fortuitous circumstances of the physical environment (extrapensatory mortality) may thus either precede or follow the compensatory stage depending on whether adults or eggs are subject to large density-independent losses. The sequence of types of mortality can be varied, but for the present purpose it is assumed that compensation precedes any extrapensatory climatic effect.

For sockeye or coho salmon, which spend a year or more in fresh water, there are further opportunities in the juvenile stages for compensatory mortalities where the number of individuals may exceed the rearing capacity of the environment. Again the sequence of the model can be varied to suit the circumstances to be simulated. For the present discussion it will be assumed that compensation also forms one of a number of possibilities in the rearing stage.

The formula of Ricker (1954) for compensation has a rationale related to cannibalism or density-dependent predation and is described by equation (1). At stock densities greater than 1, compensation may be unrealistically severe. Following Ward and Larkin (1964), provision is made as an alternative for use, over stock densities of 1, of the relation,

$$Z = (1-D)e^{-a_2(W-1)} + D \qquad (9)$$

in which the value a_2 may be called a "saturation coefficient" and which is asymptotic at D for infinite values of W. The output of this first life history stage represents the potential production of fry (Z).

Extrapensatory Mortality

The effects of fluctuating environmental conditions scaled to any particular order of magnitude may be simulated in the manner described by Ricker (1954). Instead of using tabled values, random normal deviates (RND) can be generated in a computer by summing twelve random deviates uniform in the range $-\frac{1}{2}$ to $+\frac{1}{2}$ (Leslie and Gower, 1958). To simulate environmental fluctuations, the random normal deviates are augmented in absolute value by unity, then used as multipliers if the sign is positive or divisors if negative (Ricker, 1954). Scaling the deviates to produce a specified ratio of extreme values is accomplished by multiplying by a factor before the deviate is augmented in absolute value (Ricker, 1954; Ward and Larkin, 1964).

Use of random normal deviates in the fashion described above is based on the observation that in natural stocks the *modus operandi* of environmental effects tends to produce a skewed distribution of observed recruitments for a particular stock size. As an alternative it may be provided that the deviations are symmetrically distributed about the mean, making them additive rather than multiplicative. The value of this type and other types of simulation of environmental effects has not been examined.

Recognizing that various stocks may encounter different orders of magnitude of environmental effects, the model makes provision for separate scaling factors (Q_{1k}) for each stock. It is also assumed that there is no relation between the

environmental effects on the various stocks in a particular brood year, each stock in a given year being influenced by a different random normal deviate.

After modification (multiplication or division) by simulated environmental effects, for each stock (k) the potential crop of fry (Z) becomes (in simulation) the actual production of fry (R).

Viz.

$$\left.\begin{aligned} R &= Z(|RND| \cdot Q_1 + 1) \text{ where RND is positive} \\ R &= Z/(|RND|\ Q_1 + 1) \text{ where RND is negative} \end{aligned}\right\} \quad (10)$$

where RND is a random normal deviate drawn from a unit normal distribution with mean zero.

Depensatory Mortalities

A variety of types of depensatory mortality may be represented in "reproduction curve" diagrams[2], depicting what the relation would be between input and output if they were the only factors operating in the life history (Larkin *et al.*, 1964). A convenient expression is a "converse" of Ricker's compensation formula, given by

$$\begin{aligned} M &= Re^{a_3(R-1)}, R < 1 \\ M &= R \qquad\quad , R > 1 \end{aligned} \quad (11)$$

where M is the production of smolts
R is the actual production of fry
a_3 is a coefficient of depensation.

The value of the exponential constant a_3 may be fixed if one visualizes, for example, a fixed population of predators, which crops a small prey population more heavily than a large one. It may alternatively be envisaged that the rate of depensatory mortality is influenced by the density of prey in a certain number of previous years. In this case the value a_3 may be a function of the densities of previous year-classes. Ward and Larkin (1964) employed such a device as an integral part of a model simulating the phenomenon of cyclic dominance in sockeye salmon. Their value a_3 was determined by the relation,

$$a_3 = F_1 \cdot E_{t-1} + F_2 \cdot E_{t-2} + F_3 \cdot E_{t-3} \quad (12)$$

where E_{t-1} are the escapements of adults in the three previous years and
F_1 are coefficients relating previous years escapements to the rate of depensation.

It was envisaged that predators prospered on eggs and fry produced by previous broods, and that the appropriate single index of this food supply was the size of spawning escapement which produced it.

In the present model provision is made for two, more precisely defined types of density-influenced rates of depensation. For both, the value a_3 is determined by a relation similar to that of equation (12), the first employing values for the

[2]The use of the phrase "reproduction curve" is a bit of a misnomer in this sense because once displaced from equilibrium, depensatory systems provide no mechanism for restoring equilibrium, the population either increasing or decreasing indefinitely.

number of eggs deposited (the $\Sigma E_t G_t$ of equation 4), the second using the values for the actual production of fry (i.e. after compensatory and extrapensatory mortality stages).

Many other kinds of depensatory processes could be substituted in the model for this simulated stage of the life history (Larkin *et al.*, 1964). A second compensatory stage may in some instances seem more appropriate (if the rearing capacity is limited). Alternatively, this life-history stage may be bypassed, the only processes relevant being the earlier ones of compensation and environmental fluctuation. Similarly, it may seem more realistic in some circumstances to insert a depensatory stage before invoking extrapensatory mortality, if for instance the spawning areas seem stable, but the rearing areas subject to environmental variation in capacity. With relatively little modification the model can be altered to provide different types and sequences of stages, with different parameters for each of the various stocks.

The output, at this point in the life history, is a simulation of the number of smolts in the run.

Smolt Buffered Depensation

For sockeye salmon, there exists the possibility of a particular kind of population interaction between broods of successive years. Smolts of one year-class leave the rearing lake at about the same time as the fry-of-the-year emerge. Where the fry emergence is near the lake outlet, predation on the fry is buffered by the presence of the seaward migrating smolts. This phenomenon was simulated in the model for cyclic dominance of Ward and Larkin (1964) and is a useful device for providing simulation of a "sub-dominant" run in the year following the dominant run. The buffering effect can be simplified as a supplement to the "biomass" units of fry which are to be processed through depensation. The provisional quantity (B) is first formed:

$$B = R + S_B \cdot M_{t-1} \tag{13}$$

where B is the simulated biomass in fry units

R is the number of fry in the current year

M_{t-1} is the number of *smolts* produced from the previous brood

S_B is a coefficient relating smolt biomass to fry biomass.

The quantity B is then processed through a depensatory stage such as that given in equation (11), and the resultant output may then be divided in proportion to the relative contributions of fry and smolts to the value of B. This procedure expressed in a single stage is:

$$M = Re^{a_1(B-1)}, \quad B < 1 \tag{14}$$

$$M = R \qquad , \quad B > 1$$

where M is the production of smolts arising from a brood of fry, predation on which was buffered by the previous brood of smolts (M_{t-1}).

The model provides that each stock may or may not have smolt buffered depensation.

Marine Life-History Stage

The simulation of mortalities in that stage of the life-history between seaward migration and ultimate return could assume a variety of forms. In the absence of any evidence for severe compensatory or depensatory mortality, provision at present is only made for extrapensatory types of factor. Following a similar procedure as in the freshwater stage (equation 10) scaled (Q_2) random normal deviates are used to simulate extrapensatory effects. In the marine stage it seems appropriate to consider that all stocks of a river system should share the same random modifier in a particular generation, and the model provides accordingly.

After this extrapensatory modification the productions for the various stocks, in stock units, may now be called the *marine production* (N_k)[3], from which proportions are drawn for the runs of mature fish in appropriate succeeding calendar years. The proportions which mature at various ages are determined by the proportions of fish of various ages that were in the parent escapement (the $Pmat_t$ of equation 7, with modifications as outlined).

APPLICATIONS OF THE MODEL

An Example — Cyclic Dominance

A stage of depensatory mortality, the severity depending on the size of runs of previous years, can be used as a device for simulating cyclic dominance in a sockeye salmon run (Ward and Larkin, 1964). An example of this kind is useful in describing some of the aspects of the general model described in previous sections.

A single stock is envisaged in which 4-year-old fish predominate (3-year-olds 8%; 4's 90%; 5's 2%). Initial conditions provide for six previous years in which this age composition prevails, and in which the spawning population sizes in stock units are 0.01, except that of four years previous (the dominant line) which is 0.1, i.e. ten times as large. Each generation comprises in sequence a stage of compensation, extrapensatory effects, a depensatory stage (equation 11), and a second (marine) extrapensatory effect. Depensatory mortality is not buffered by smolts. Random normal deviates are used as multipliers or divisors. There is no simulated fishery.

The values of the pertinent parameters are:

$G_{3,4,5}$	(fecundity factors for ages 3, 4, 5)	0.8, 1.0, 1.0
J	(jack factor)	1.0
a_1	(egg compensation coefficient)	2.0
a_2	(saturation coefficient)	2.0
D	(compensation asymptote)	0.75
Q_1	(freshwater extrapensatory scaling coefficient)	0.20715
$F_{1,2,3}$	(depensation coefficients related to spawning stock sizes of 1, 2, and 3 years previous)	4.0, 4.0, 4.0
Q_2	(marine extrapensatory scaling coefficient)	0.61803.

[3]In a pseudo-simulation of the chronology of events the computer program for the model at this point stores the figures for marine production and skips to the reconstruction of another adult run.

TABLE II. Age composition and spawning population size in stock units for a series of years in simulation of severe quadrennial cyclic dominance as caused by depensatory mortality related in intensity to sizes of populations in three previous years.

	Age			
Year	3	4	5	Total
1	.0008	.0900	.0002	.0910
2	.0008	.0090	.0020	.0118
3	.0008	.0090	.0002	.0100
4	.0068	.0090	.0002	.0160
5	.0039	.7654	.0002	.7695
6	.0025	.0441	.0017	.0483
7	.0294	.0289	.0098	.0682
8	.0063	.0389	.0006	.0459
9	.0009	1.2400	.0008	1.2400
10	.0573	.0156	.0003	.0733
11	.0100	.0563	.0006	.0669
12	.0008	.0616	.0190	.0815
13	.0120	1.1930	.0010	1.2060
14	.0018	.0032	.0008	.0059
15	.0008	.0101	.0000	.0110
16	.0099	.0610	.0001	.0710
17	.0000	.9800	.0189	.9989
18	.0000	.0000	.0008	.0009
19	.0069	.0007	.0000	.0078
20	.0000	.0430	.0000	.0430
21	.0000	.3068	.0000	.3068
22	.0008	.0000	.0059	.0067
23	.0000	.0000	.0001	.0002
24	.0000	.0168	.0000	.0169
25	.0026	.7217	.0000	.7243
26	.0000	.0000	.0001	.0002
27	.0000	.0001	.0183	.0185
28	.0056	.0484	.0002	.0543
29	.0000	1.5460	.0000	1.5460
30	.0000	.0000	.0000	.0001
31	.0077	.0001	.0000	.0080
32	.0000	.0662	.0202	.0864
33	.0000	1.3060	.0003	1.3060
34	.0000	.0000	.0000	.0000
35	.0000	.0000	.0000	.0000
36	.0000	.0368	.0000	.0368
37	.0000	1.1700	.0112	1.1810
53	.0000	.5450	.0000	.5450
54	.0000	.0000	.0000	.0000
55	.0000	.0000	.0000	.0000
56	.0000	.0000	.0000	.0000

Segments of a 120-year simulation (Table II) indicate the development of strong quadrennial cyclical dominance on the cycle years 1, 5, 9, 13 and so on. With no smolt buffering there is no suggestion of a sub-dominant run in the year following the dominant cycle. Inheritance of age of maturity of progeny on the basis of age composition of a parent escapement results in rapid elimination of 3's and 5's, so that by the years 53–56, the stock is composed of a pure strain of 4-year-old fish returning on the dominant cycle years. This is to be expected, for the severe effects of depensation in the "off-years" consistently eliminate the 3's and 5's.

The relatively large fecundity factor for 3's of 0.8 implies that jacks contribute substantially to production, and this helps preserve the 3's in the population on a 3-year cycle, the years 4, 7, 10 . . . . . 25, 28, 31. The 5's fluctuate in a 5-year cycle on the years 2, 7, 12 . . . . . 27, 32, 37. But both 3's and 5's coincide so seldom in their cycles with the abundant 4's, that they are soon eliminated.

The example is obviously exaggerated, because the determination of age in the model is entirely attributed to inheritance and the effects of depensation are severe. It nevertheless serves to indicate the value of the inheritance feature of the model in suggesting a way in which selection of a particular age could proceed, and quite rapidly.

An Example — Harvesting of Mixed Stocks

In its computer program counterpart, the model is designed for simulating the complex of events when a fishery, which is differentially selective for different ages of fish, harvests jointly a number of stocks, each of which has a characteristic age distribution and its own early life-history environment.

Five stocks are envisaged, which share a common marine life and are exposed jointly to the same fishery. The initial conditions provide that all stocks are at equilibrium at one stock unit at all stages of the life history, and have been for as many years previous as are necessary to begin a simulation from a deterministic system at equilibrium. This initial equilibrium condition pertains also to age composition and fecundity figures. Thus, in the absence of a fishery the age composition and stock sizes would be constant in a deterministic model, and would fluctuate about the constant value in the stochastic model simulating environmental effects. For the five stocks the data input for pertinent initial conditions are given in the first half of Table III.

The second half of Table III lists the pertinent operating constants for each of the stocks. The values chosen describe a situation in which one stock (stock 1) is much larger in order of magnitude and has a higher compensation coefficient ($a_1 = 2$) than the other stocks for which $a_1 = 1$, and contains more 4-year-olds than 5's. The second stock is one-half as large and has more 5's than 4's. The other three stocks are one-tenth the size of stock 1, and two of them (stocks 3 and 4) have proportionately more 6-year-olds, while the last (stock 5) has a similar age composition to stock 1. Differences in stock size and age composition of this kind are not unlike natural situations such as the Skeena River (Shepard and Withler, 1958).

TABLE III. Initial conditions and operating constants for example illustrating harvesting of mixed stocks.

	Stock				
Parameters	1	2	3	4	5
Initial conditions					
$Pmat_3$	0.10	0.11	0.12	0.12	0.10
$Pmat_4$	0.45	0.34	0.32	0.32	0.45
$Pmat_5$	0.40	0.49	0.35	0.35	0.40
$Pmat_6$	0.05	0.06	0.21	0.21	0.05
G_3	0.0180	0.0180	0.0180	0.0180	0.0180
G_4	1.0560	1.0560	1.0560	1.0560	1.0560
G_5	1.1554	1.1554	1.1554	1.1554	1.1554
G_6	1.2180	1.2180	1.2180	1.2180	1.2180
$M_1 - M_6$	1.0	1.0	1.0	1.0	1.0
$W_1 - W_6$	1.0	1.0	1.0	1.0	1.0
V	10.0	5.0	1.0	1.0	1.0
J	0.3711	0.3711	0.3711	0.3711	0.3711
a_1	2.0	1.0	1.0	1.0	1.0
Q_1	0.20715	0.20715	0.20715	0.20715	0.20715
Q_2	0.61803	0.61803	0.61803	0.61803	0.61803
E	←		total 7.074		→
S_3	0.0	0.0	0.0	0.0	0.0
S_4	0.8	0.8	0.8	0.8	0.8
S_5	1.0	1.0	1.0	1.0	1.0
S_6	0.9	0.9	0.9	0.9	0.9

There is no stage of depensation for any of the stocks, nor is it envisaged that there is any asymptotic recruitment reflecting ameliorating effects of compensation at high stock densities. Thus for each stock the sequence of life-history stages is as in the models of Ricker (1954, 1958) with compensation according to equation (1). The major difference from the Ricker models is the double sequence of random normal deviates, the first affecting each stock separately (scaled by a coefficient of 0.20715 for two-fold ratio of extremes) and the second (marine) affecting all stocks jointly (scaled by 0.61803 for five-fold ratio of extremes)[4].

The operation of the fishery is based on complete stabilization of escapement of the stocks *when fished as a whole.* As a first approximation, the optimum escapement for the stock taken as a whole may be calculated as the sum of the optimum escapements for each of the stocks taken separately, with appropriate multiplication by factors of order of magnitude (Table IV).

In the operation of the fishery, the actual distribution of escapements will depart from the schedule of Table IV, because the stocks in a joint fishery are harvested at a common average rate. This rate will be somewhat less than that

[4]The resultant of these two operations involving random normal deviates is a distribution similar in form but with a ratio of extremes of 5.3064 to 1. Hence the double extrapensatory stage is not a fundamental departure from the Ricker procedure, except that it provides by virtue of the second stage, a degree of interdependence in the fluctuations of the stocks.

TABLE IV. Optimum escapements for stocks being harvested used to approximate the optimum escapement for the combined run in a joint fishery.

Stock	Magnitude	Optimum escapement in stock units	Optimum escapement from fishery
1	10	0.361	3.610
2	5	0.433	2.165
3	1	0.433	0.433
4	1	0.433	0.433
5	1	0.433	0.433
		Optimum escapement, joint fishery = 7.074	

for maximum equilibrium yield for stock 1 (72.9%) and more than that for stocks 2 to 5 (43.3%). In consequence the eventual equilibrium escapements are below the optimum for stocks 2 to 5 and above the optimum for stock 1. An exact solution for this equilibrium state, and that which would be associated with maximum equilibrium yield, is not attempted here, and in the example, the first approximation of joint optimum escapement (Table IV) is used for the operation of the fishery.

Selectivity for age of fish is based on the coefficients for 3-, 4-, 5-, and 6-year-old fish of 0.0, 0.8, 1.0, and 0.9, respectively. Because there is no fishery on jacks, a jack factor is necessary in the calculation of proportions of fish maturing at different ages. The value of 0.371 is the complement for the fishing rate of 0.629, and would serve to keep the proportion of jacks constant despite their absence from the fishery.

The results of a series of 120 years are summarized in Table V in which data are given for every tenth year[5] throughout the 120-year period. The yearly abundance of the run, catch, and spawning escapement is shown (in stock units) for each of the five stocks in Fig. 2. The relative abundance of 3-, 4-, 5-, and 6-year-old fish is shown for each stock in each year in Fig. 3. Comparisons between stocks illustrate the effects of several processes incorporated in the model, namely:

1. *Fortuitous environmental effects.* The initial and operating conditions for stocks 3 and 4 are identical except for the extrapensatory environmental effects of their freshwater environment (Table III). Their relative abundance fluctuates initially with neither stock becoming more than twice as abundant as the other for the first 50 years (Fig. 2, Table V). After year 50, stock 3 apparently receives a more favourable series of random deviates and is more abundant than stock 4 in almost every year for the next 50 years. The effect of the random deviates is then reversed and after year 100, stock 4 regains a level of abundance similar to that of stock 3.

[5]Copies of the results for 120 years are on file at the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.

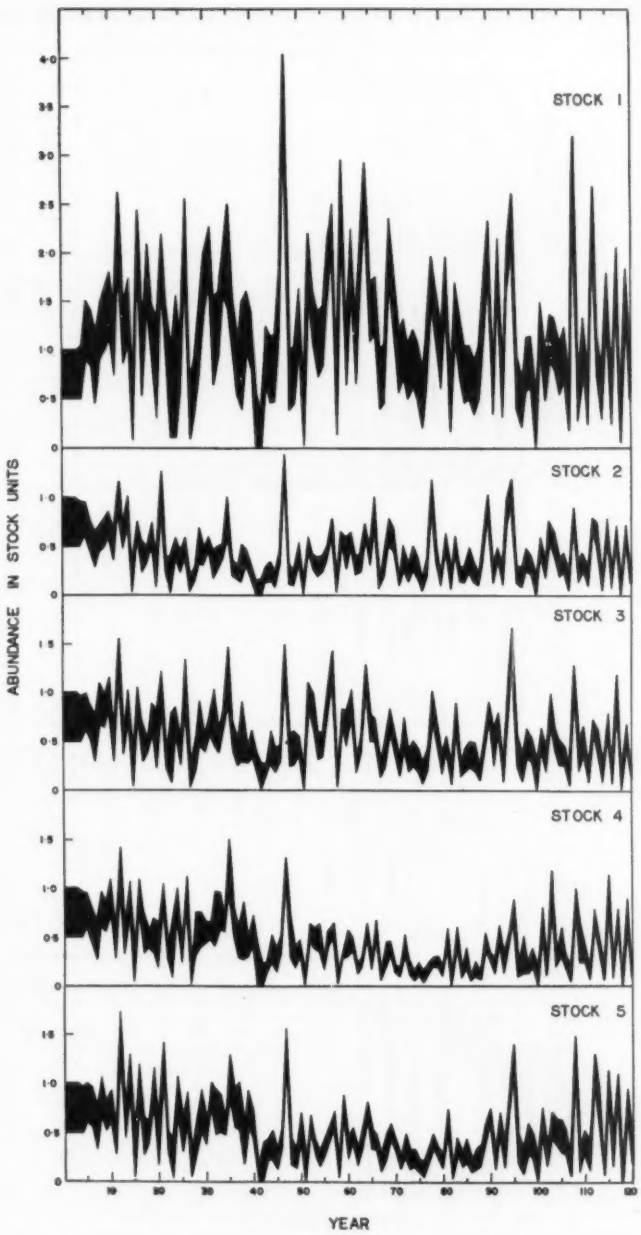


FIG. 2. Abundance of the run (top line), catch (bottom line), and spawning escapement (difference between top and bottom lines shown as shaded area) in stock units for each of five stocks through a 120-year simulation by the model for harvesting of mixed stocks.

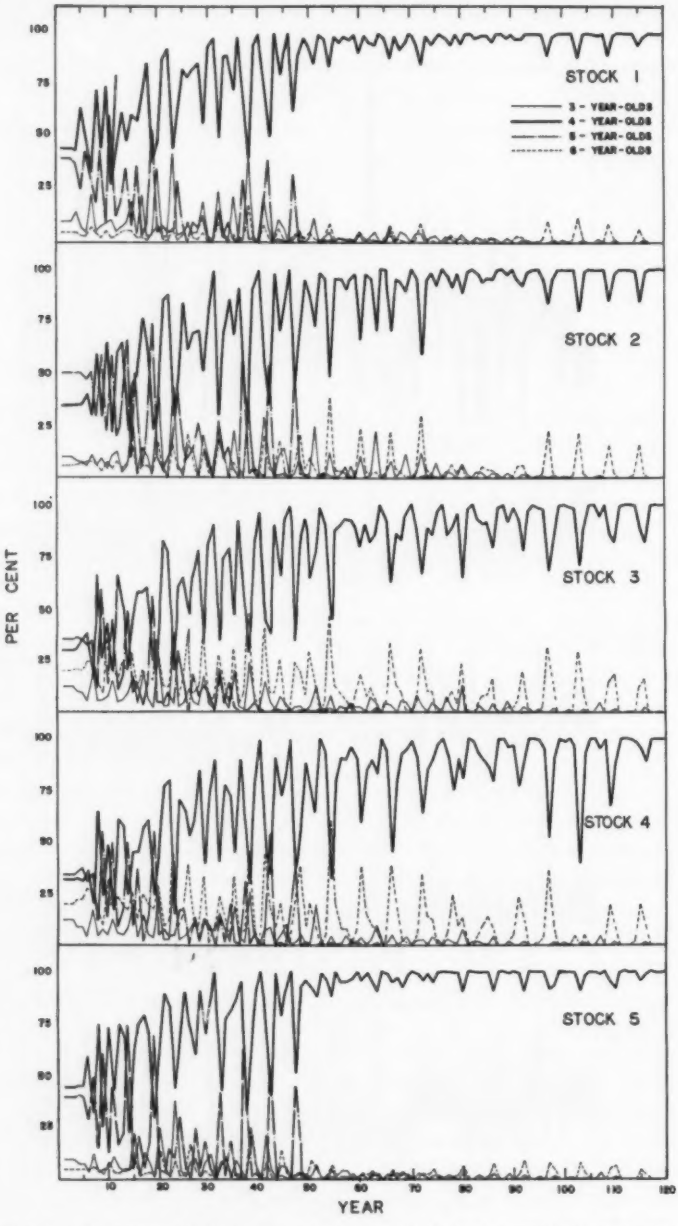


Fig. 3. Percentage of 3-, 4-, 5-, and 6-year-old fish in the runs for five stocks through a 120-year simulation by the model for harvesting of mixed stocks.

TABLE V. The first and every tenth year of a 120-year simulation of harvesting mixed stocks.

Year	Stock	Run					Catch					Escapement				
		Age					Age					Age				
		3	4	5	6	Total	3	4	5	6	Total	3	4	5	6	Total
1	1	.1000	.4500	.4000	.0500	1.0000	0.0000	.2261	.2490	.0840	.5011	.1000	.2239	.1510	.0219	.4988
	2	.1100	.3600	.4900	.0600	1.0000	0.0000	.1694	.3050	.0336	.5080	.1099	.1706	.1850	.0564	.4919
	3	.1300	.3900	.3500	.2100	1.0000	0.0000	.1994	.2178	.1174	.4946	.1299	.1606	.1322	.0904	.5051
	4	.1300	.3900	.3500	.2100	1.0000	0.0000	.1994	.2178	.1174	.4946	.1299	.1606	.1322	.0904	.5051
	5	.1000	.4500	.4000	.0500	1.0000	0.0000	.2261	.2490	.0840	.5011	.1000	.2239	.1510	.0219	.4988
	All	.5500	1.8800	1.9900	.5800	5.0000	0.0000	.7966	1.2380	.3348	2.4960	.5497	.8636	.7514	.2550	2.4196
10	1	.1698	1.3460	.1952	.1053	1.8110	0.0000	.8971	.1638	.0798	1.1380	.1697	.4490	.0334	.0263	.6734
	2	.0773	.5597	.1994	.0643	.8549	0.0000	.3708	.1643	.0484	.5835	.0773	.1889	.0331	.0161	.3154
	3	.0898	.4959	.1823	.4894	1.2640	0.0000	.3309	.1355	.3073	.7737	.0898	.1650	.0270	.1821	.3749
	4	.0949	.5303	.1490	.3544	1.0800	0.0000	.3472	.1242	.2676	.7390	.0949	.1771	.0248	.0888	.3410
	5	.0600	.4616	.1127	.0775	.9308	0.0000	.4549	.0931	.0588	.6068	.0600	.1867	.0186	.0193	.3846
	All	.3988	3.3970	.8178	1.0130	5.8220	0.0000	2.3980	.6819	.7607	3.8370	.3967	1.1980	.1369	.2526	1.9810
20	1	.4647	.8233	.0682	.1671	1.3250	0.0000	.2868	.0306	.0675	.3229	.4645	.6005	.0375	.0996	1.0020
	2	.1521	.1489	.0981	.0704	.4693	0.0000	.0934	.0171	.0288	.0990	.1520	.0953	.0209	.0419	.3101
	3	.2472	.2503	.0431	.2836	.8088	0.0000	.0900	.0803	.1155	.2858	.2471	.1603	.0268	.1701	.6023
	4	.1572	.2700	.0348	.1770	.6390	0.0000	.0971	.0156	.0715	.1842	.1571	.1729	.0192	.1055	.4547
	5	.1379	.2722	.0256	.0849	.6206	0.0000	.1338	.0114	.0351	.1803	.1378	.1734	.0160	.0517	.4619
	All	1.1790	1.6648	.2116	.7870	3.8380	0.0000	.5991	.0951	.3181	1.0120	1.1770	1.0670	.1164	.4688	2.8220
30	1	.0536	1.8900	.0852	.0117	2.0360	0.0000	1.3080	.0494	.0091	1.3660	.0536	.5830	.0107	.0026	.6509
	2	.0443	.7989	.0413	.0139	.4985	0.0000	.2761	.0257	.0108	.3226	.0443	.1228	.0093	.0050	.1757
	3	.0235	.4815	.0834	.0979	.5953	0.0000	.3306	.0454	.0295	.4085	.0235	.1479	.0070	.0083	.1867
	4	.0315	.4867	.0597	.0650	.6429	0.0000	.3373	.0517	.0507	.4395	.0315	.1496	.0080	.0143	.2034
	5	.0741	.4997	.0348	.0101	.6187	0.0000	.3461	.0301	.0079	.3841	.0740	.1536	.0046	.0022	.2344
	All	.2692	3.7540	.2845	.1387	4.4050	0.0000	2.6000	.2525	.1081	2.9350	.2490	1.1550	.0559	.0506	1.4660
40	1	.0048	1.3620	.0098	.0027	1.3780	0.0000	.7997	.0072	.0026	.8053	.0048	.5670	.0026	.0012	.5756
	2	.0003	.0824	.0041	.0007	.0855	0.0000	.1638	.0030	.0004	.1672	.0003	.1166	.0011	.0002	.1182
	3	.0021	.0915	.0057	.0139	.1162	0.0000	.3592				.0021	.2457	.0015	.0047	.2550
	4	.0023	.0429	.0056	.0125	.7131	0.0000	.4049	.0041	.0021	.4171	.0023	.2880	.0015	.0042	.2960
	5	.0011	.0904	.0040	.0023	.6978	0.0000	.4035	.0029	.0015	.4079	.0011	.2869	.0010	.0007	.2897
	All	.0110	3.6150	.0294	.0332	3.6850	0.0000	2.1120	.0215	.0218	2.1520	.0117	1.5050	.0079	.0113	1.5300
50	1	.0315	1.5290	.0093	.0457	1.6280	0.0000	.9899	.0018	.0474	1.0300	.0315	.5490	.0006	.0182	.5993
	2	.0099	.4478	.0021	.0467	.5090	0.0000	.2864	.0018	.0537	.3325	.0099	.1606	.0004	.0130	.1839
	3	.0148	.3782	.0099	.1309	.5319	0.0000	.2126	.0023	.1099	.3249	.0148	.1356	.0005	.0419	.1972
	4	.0066	.3623	.0017	.0992	.4708	0.0000	.2231	.0014	.0717	.3062	.0066	.1302	.0003	.0273	.1646
	5	.0098	.6269	.0013	.0448	.7082	0.0000	.4881	.0010	.0448	.4499	.0098	.2244	.0002	.0140	.2528
	All	.0727	3.3438	.0116	.4285	3.8530	0.0000	2.1440	.0093	.3094	2.4570	.0726	1.1980	.0025	.1191	1.3950
60	1	.0534	1.0990	.0019	.0622	1.2150	0.0000	.6038	.0013	.0384	.6435	.0534	.4960	.0005	.0237	.5736
	2	.0613	.3950	.0005	.1260	.5928	0.0000	.2170	.0003	.0840	.3013	.0613	.1780	.0001	.0520	.2914
	3	.0209	.6518	.0010	.1493	.8230	0.0000	.3580	.0007	.0922	.4509	.0209	.2938	.0002	.0971	.3721
	4	.0183	.3384	.0005	.2152	.5724	0.0000	.1857	.0003	.1329	.3189	.0183	.1527	.0001	.0823	.2534
	5	.0096	.4408	.0003	.0123	.4630	0.0000	.2421	.0002	.0076	.2499	.0096	.1987	.0001	.0047	.2131
	All	.1635	2.9250	.0044	.5750	3.6620	0.0000	1.6050	.0030	.3552	1.9590	.1635	1.3180	.0013	.2198	1.6990
70	1	.0046	1.7850	.0024	.0002	1.7910	0.0000	1.2250	.0001	.0001	1.2270	.0046	.5600	.0003	0.0000	.5649
	2	.0009	.4856	.0004	.0001	.4870	0.0000	.4706	.0004	0.0000	.4710	.0009	.2150	0.0000	0.0000	.2159
	3	.0020	.5830	.0008	.0007	.5867	0.0000	.4003	.0007	.0005	.4015	.0020	.1829	.0001	.0001	.1851
	4	.0016	.2187	.0005	.0007	.2155	0.0000	.1458	.0005	.0006	.1469	.0016	.0669	0.0000	.0001	.0687
	5	.0013	.4547	.0002	.0002	.4566	0.0000	.3119	.0002	.0001	.3122	.0013	.1428	0.0000	0.0000	.1441
	All	.0105	3.7190	.0046	.0021	3.7310	0.0000	2.5510	.0059	.0016	2.5530	.0105	1.1660	.0008	.0004	1.1770
80	1	.0477	1.2090	.0008	.0830	1.2760	0.0000	.6058	.0003	.0334	.6197	.0477	.6030	.0003	.0496	.6196
	2	.0177	.2343	.0001	.0158	.2699	0.0000	.1183	0.0000	.0099	.1274	.0177	.1178	0.0000	.0046	.1423
	3	.0513	.2374	.0003	.0983	.4093	0.0000	.1391	.0003	.0533	.1884	.0513	.1243	.0001	.0411	.2208
	4	.0145	.1434	.0001	.0057	.1837	0.0000	.0830	0.0000	.0145	.0966	.0145	.0856	0.0000	.0112	.1071
	5	.0100	.3760	.0001	.0197	.3058	0.0000	.1384	0.0000	.0111	.1495	.0100	.1376	0.0000	.0086	.1562
	All	.1413	2.1990	.0016	.1778	2.4550	0.0000	1.0730	.0010	.1004	1.1710	.1413	1.0670	.0005	.0776	1.2820
90	1	.0056	2.3090	.0008	.0128	2.3280	0.0000	1.7710	.0008	.0110	1.7830	.0056	.5380	0.0000	.0017	.5453
	2	.0029	1.0290	.0001	.0148	1.0468	0.0000	.7890	.0001	.0093	.7984	.0029	.2600	0.0000	.0014	.2643
	3	.0028	.8737	.0002	.0181	.8948	0.0000	.6913	.0002	.0136	.6971	.0028	.2044	0.0000	.0015	.2087
	4	.0027	.7511	.0001	.0153	.3692	0.0000	.2699	.0001	.0132	.2832	.0027	.0822	0.0000	.0021	.0850
	5	.0009	.7585	0.0000	.0013	.7607	0.0000	.5817	0.0000	.0011	.5828	.0009	.1768	0.0000	.0001	.1778
	All	.0130	5.3220	.0013	.0585	5.3920	0.0000	4.0810	.0013	.0504	4.1300	.0130	1.2600	0.0000	.0080	1.2590
100	1	.0038	.5193	0.0000	.0001	.5192	0.0000	.0004	0.0000	0.0000	.0004	.0038	.5099	0.0000	.0001	.5138
	2	.0013	.2900	0.0000	0.0000	.2913	0.0000	.0004	0.0000	0.0000	.0004	.0013	.2896	0.0000	0.0000	.2909
	3	.0016	.3180	0.0000	.0004	.3160	0.0000	.0003	0.0000	0.0000	.0003	.0016	.3089	0.0000	.0004	.3109
	4	.0030	.2191	0.0000	.0003	.2226	0.0000	.0003	0.0000	0.0000	.0003	.0030	.2168	0.0000	.0003	.2201
	5	.0012	.2978	0.0000	0.0000	.2990	0.0000	.0001	0.0000	0.0000	.0001	.0012	.2947	0.0000	0.0000	.2959
	All	.0111	1.5950	0.0000	.0009	1.6060	0.0000	.0019	0.0000	0.0000	.0019	.0111	1.5760	0.0000	.0009	1.5870
110	1	.0072	1.3040	0.0000	.0002	1.3110	0.0000	.7537	0.0000	.0135	.7668	.0072	.5510	0.0000	.0070	.5652
	2	.0016	.4233	0.0000	.0002	.4271	0.0000	.2399	0.0000	.0066	.2465	.0016	.1774	0.0000	.0036	.1886
	3	.0040	.5371	0.0000	.1149	.6560	0.0000	.3183	0.0000	.0717	.3850	.0040	.2268	0.0000	.0432	.2793
	4	.0031	.3991	0.0000	.0475	.4519	0.0000	.2306	0.0000	.0308	.2614	.0031	.1685	0.0000	.0166	.1906
	5	.0069	.5077	0.0000	.0261	.5907	0.0000	.2933	0.0000	.0234	.3167	.0069	.2144	0.0000	.0126	.2339
	All	.0293	3.1620	0.0000	.1889	3.4180	0.0000	1.8360	0.0000	.1680	1.9720	.0293	1.3350	0.0000	.0831	1.4630
120	1	.0022	1.0580	0.0000	.0008	1.0580	0.0000	.4959	0.0000	.0004	.4963	.0022	.5730	0.0000	.0004	.5736
	2	.0001	.3066	0.0000	.0010	.3077	0.0000	.1408	0.0000	.0005	.1413	.0001	.1658	0.0000	.0005	.1664
	3	.0001	.2919	0.0000	.0012	.2932	0.0000	.1360	0.0000	.0006	.1366	.0001	.1579	0.0000	.0006	.1586
	4	.0001	.2211	0.0000	.0008	.2260	0.0000	.1015	0.0000	.0004	.1029	.0001	.1196	0.0000	.0013	.1210
	5	0.0000	.4897	0.0000	.0001	.4898	0.0000	.2233	0.0000	0.0000	.2233	0.0000	.2634	0.0000	0.0000	.2634
	All	.0027	2.3620	0.0000	.0052	2.3660	0.0000	1.0880	0.0000	.0032	1.0880	.0027	1.2790	0.0000	.0030	1.2810

2. *Effects of a joint fishery.* The relative over-harvesting of stocks 2 to 5 which results from their mixture with the more productive stock 1 in the fishery is evident almost immediately. They all persist throughout the 120-year simulation but at average escapements below the optimum of 0.433 stock units (Table V). Conversely, stock 1 is maintained at average escapements in excess of the optimum of 0.361 stock units.

3. *Effects of fishing selectivity on age composition.* The fishery is most effective at removing 5-year-old fish (S = 1.0) and more effective at removing 6-year-old fish (S = 0.9) than 4-year-old fish (S = 0.8). Consequently, the escapement of 5-year-old fish becomes progressively smaller, reaching zero for all stocks in one cycle at year 66. By year 113, 5-year-old fish disappear from all cycles (Fig. 3). Six-year-old fish also gradually disappear from the run, but at a slower rate. (The numbers of 6-year-old fish become zero for stocks on one cycle in year 118[6] and are approaching zero in all other cycles.) On the other hand, the proportion of 4-year-old fish in the various stocks increases continuously (aside from the random environmental effects) from between 32 and 45% in year 1 to between 69 and 94% in year 50. After year 50, 4-year-old fish make up over 90% of all stocks in most years.

4. *Combined effects of fishing selectivity and age composition on the relative abundance of stocks.* The initial and operating conditions for stocks 3, 4, and 5 are identical except for age composition (Table III), stocks 3 and 4 containing proportionately more older fish. The fishery is more selective for 5- and 6-year-old fish, and initially overfishes stocks 3 and 4 more than stock 5. Thus stock 5 tended to be larger than either stock 3 or stock 4 over most of the period during which 5- and 6-year-old fish were present in significant numbers (i.e. to about year 50, Fig. 2). Subsequently, selection having reduced all of the stocks to a common preponderance of 4-year-olds, there are no longer measurable effects of age composition on abundance.

Other Applications

With use of various optional procedures the model may be used to simulate a wide variety of population phenomena characteristic of salmon or other species of animals. The variable number of life-history stages and the types of mortality which occur in them provide sufficient flexibility to be descriptive of many kinds of situations. Similarly, the circumstances of operation of a fishery can be sufficiently varied to examine the consequences of several kinds of management. For instance, a particularly novel application is the possibility of empirical study of the problem of maximizing yield in a joint fishery on several stocks of several species. The simple associative nature of the reproduction curve concept is perhaps the major weakness of the model. However, in the absence of sufficient quantitative information on the mechanisms involved in population regulation at each life-history stage, the gross associations seem to provide the best basis at present for developing hypotheses of management.

[6]Actual value for stock 3 is .0001.

ACKNOWLEDGMENTS

The first plans for this model arose from discussions between Dr F. J. Ward and the senior author. During the development of the model we received valuable comments and suggestions from F. C. Withler, M. P. Shepard, J. McDonald, R. R. Parker and H. Smith. Dr W. E. Ricker made helpful editorial suggestions. These various contributions were much appreciated.

REFERENCES

GODFREY, H. 1958. A comparison of sockeye salmon catches at Rivers Inlet and Skeena River, B.C., with particular reference to age at maturity. *J. Fish. Res. Bd. Canada*, **15**(3): 331–354.

LARKIN, P. A., R. F. RALEIGH AND N. J. WILIMOVSKY. 1964. Some alternative premises for constructing theoretical reproduction curves. *J. Fish. Res. Bd. Canada*, **21**(3): 477–484.

LESLIE, P. H., AND J. C. GOWER. 1958. The properties of a stochastic model for two competing species. *Biometrika*, (45): 316–330.

RICKER, W. E. 1954. Stock and recruitment. *J. Fish. Res. Bd. Canada*, **11**(5): 559–623.

1958. Maximum yields from fluctuating environments and mixed stocks. *Ibid.*, **15**(5): 991–1006.

SHEPARD, M. P., AND F. C. WITHLER. 1958. Spawning stock size and resultant production for Skeena sockeye. *J. Fish. Res. Bd. Canada*, **15**(5): 1007–1025.

WARD, F. J., AND P. A. LARKIN. 1964. Cyclic dominance in Adams River sockeye salmon. *Intern. Pacific Salmon Fish. Comm., Prog. Rept.* No. 11, 116 pp.

A Key to Five Species of Pacific Salmon (Genus *Oncorhynchus*) Based on Scale Characters[1]

By H. T. Bilton, D. W. Jenkinson and M. P. Shepard

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

A key based on differences in scale structure was derived to separate the five North American species of Pacific salmon. For maturing individuals the key was effective in identifying precisely to species 100% of the sockeye (*Oncorhynchus nerka*), over 95% of the pinks (*O. gorbuscha*), over 90% of the chums (*O. keta*) and of the chinooks (*O. tshawytscha*), and between 14 and 67% of the coho (*O. kisutch*) examined. In all but a few of the remaining cases (in which the exact species could not be identified), the specimens were designated correctly as being one of two or three species. Only a few misclassifications (20 of the 3035 individuals examined) occurred. For sockeye the power of separation of the key for fish with only one ocean annulus was about the same as that for the matures but its ability to identify precisely chums and chinooks was lower.

INTRODUCTION

Of the six anadromous species of Pacific salmon (genus *Oncorhynchus*), five occur in North America — sockeye (*O. nerka*), pink (*O. gorbuscha*), coho (*O. kisutch*), chinook (*O. tshawytscha*), and chum (*O. keta*). The sixth species — the cherry salmon (*O. masou*) — occurs only in Asia. Means of identifying the different North American species of Pacific salmon on the basis of various body characteristics (mainly meristic counts) are described in Clemens and Wilby's extensive monograph on the "Fishes of the Pacific Coast of Canada" (1961). In many field studies necessity for rapid handling of live fish (e.g. in high-seas tagging programs) sometimes makes accurate identification of species difficult[2]. Consequently, errors in identification are frequently made by field workers. These errors come to light when salmon identified as one species at time of tagging are identified as another at time of recapture. Usually tagged salmon are recovered in coastal fishing areas where the fish are approaching full maturity and and are developing secondary sex characteristics (e.g. spawning colours, hooked snout). Under these conditions, identifications of species are more accurate than at sea. It is therefore likely that most errors in species identification in tagging experiments occur in the designation of species on the high seas. In most cases where salmon are tagged or sampled in the field, samples of scales are obtained to determine the ages of the specimens. The existence of differences in the structure of scales of different salmon species (Koo, 1962) suggested that exami-

[1]Received for publication June 17, 1964.

[2]In addition to salmon, steelhead trout (*Salmo gairdneri*) are often taken on the high seas. However, steelhead are easily separated from Pacific salmon on the basis of certain readily observable anatomical characteristics (e.g. number of anal rays, squareness of the tail, and very broad caudal peduncle).

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

nation of scale characters might provide a useful tool for checking the validity of field identifications.

A typical salmon scale (Fig. 1) is roughly oval in shape. Its outer surface bears a series of circular corrugations (circuli or sclerites) confined mainly to the anterior part of the scale. Presumably reflecting alternations of periods of rapid and slow growth during summer and winter, respectively, the circuli are alternately bunched closely together (to form so-called "annuli" or "winter" bands) and more widely spaced ("summer" bands). Gilbert (1913)[3] provided the first thorough description of the scales of the five North American species of Pacific salmon, noting consistent interspecific differences in the size of scales and in the configuration of circuli and annuli. Based on such differences, Koo (1962) devised a useful "key" for identifying the different species of North American Pacific salmon. The key was based on a relatively small number of specimens from a few areas. In the present paper, a more detailed study has been made of various scale characters. On the basis of this study a more comprehensive key was developed and by examining scales from a large number of individuals from many sampling locations, both in North America and Asia, an assessment has been made of the degree of precision in identification of species that can be expected from use of such a key.

INTERSPECIFIC DIFFERENCES IN SCALE CHARACTERS

To develop the key for separating the five North American species of Pacific salmon, the scales of almost 2000 salmon from Canadian commercial fishing areas were examined (Tables I to IV). To test the validity of the key, scales from an additional 1066 salmon from Canada, the United States, the USSR, and Japan were examined (Tables V to VIII) and processed through the key as if the species of each was unknown. In the case of both the standards and the test "unknowns", samples came from coastal areas near the spawning grounds where identification of species on the basis of other body characteristics would be quite accurate.

The following scale characteristics were examined:

(a) DIAMETER OF THE FIRST-YEAR BAND AND PRESENCE OF "FRESHWATER" CIRCULI. Pink, chum, and some chinook salmon migrate to sea shortly after emerging from the gravel, and then spend 1–5 years in the ocean before returning to fresh water to spawn. On the other hand, almost all sockeye, coho, and some chinook salmon spend at least part of their early free-swimming life in fresh water before migrating to sea. Sockeye typically spend 1 or 2 years in lakes; cohos, 1 year in streams or lakes; and many chinooks, from several months to a year in rivers. In the latter three species, the circuli in the part of the scale formed during freshwater existence are more delicate in structure and are more

[3]A paper by McMurrich, published in the same year (1913), provided a somewhat similar description but included a number of incorrect interpretations of life-history patterns.

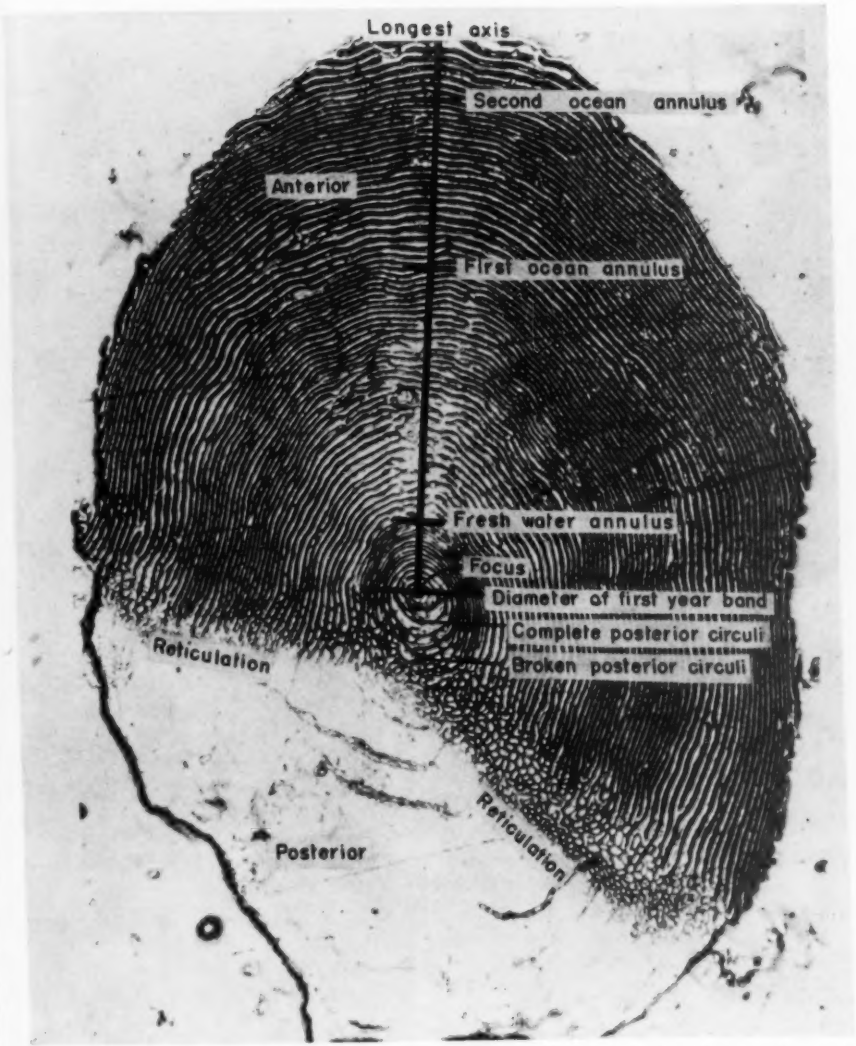


FIG. 1. Scale from an adult sockeye salmon (age 4_2) showing the location of the various scale measurements that are used.

FIG. 2. Scale from an adult sockeye salmon (age 4_2) showing the freshwater type first-year band (A_0) and ladder-like reticulation (B).

FIG. 3. Scale from an adult pink salmon (age 2_1) showing the marine type first-year band (A) and mixed ladder-like and globular reticulation (B).

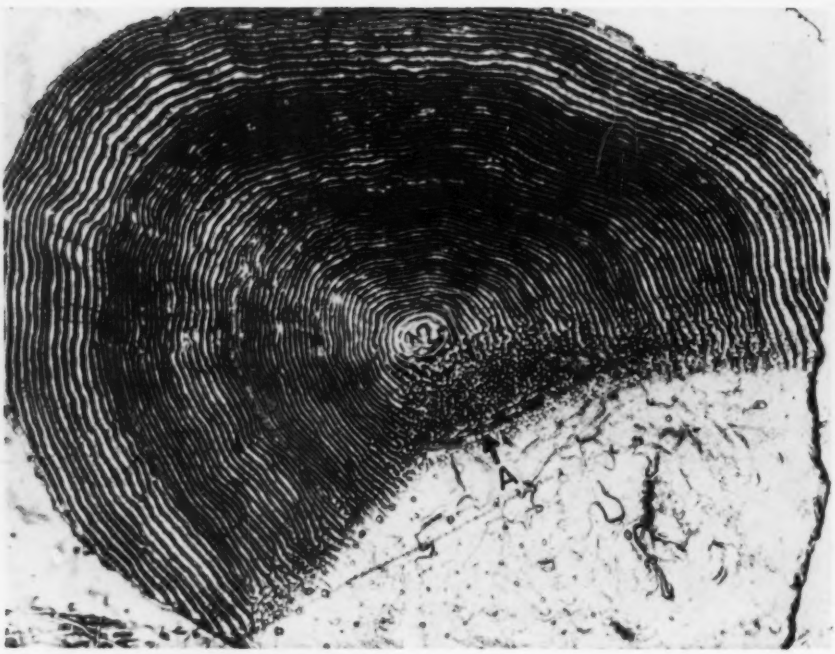


FIG. 4. Scale from an adult chum salmon (age 3_1) showing globular reticulation (A).

FIG. 5. Scale from an adult coho salmon (age 3_2) showing no reticulation (A), and the many complete and broken posterior circuli (B).

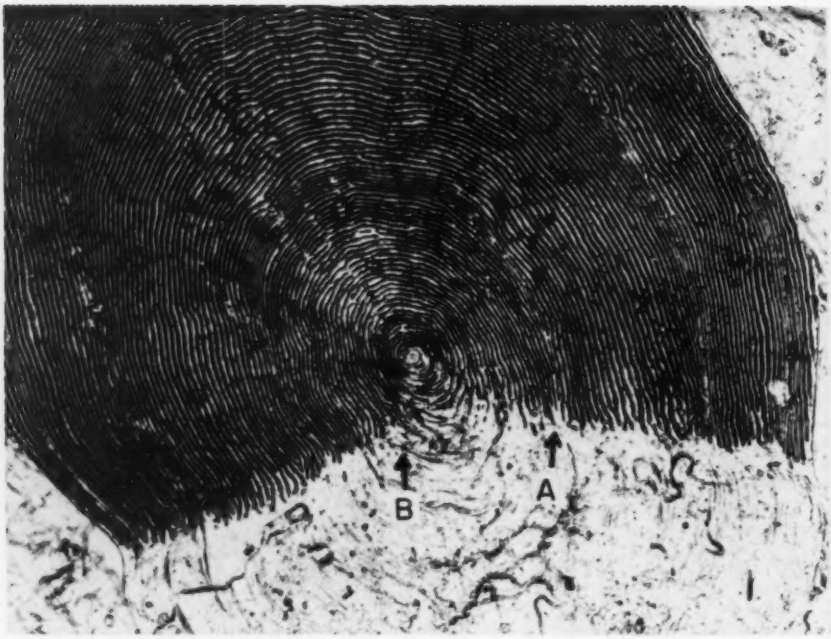


FIG. 6. Scale from an adult chinook salmon (age 4_1) showing no reticulation (A) and a moderate number of complete and broken posterior circuli (B).

Bilton *et al.* — J. Fish. Res. Bd. Canada

closely-packed than those formed early in development of species migrating to sea soon after emergence (cf. Fig. 2 and 3).

Because growth in fresh water is much less than that occurring in the sea, the interval between the focus of the scale and the first annulus is much smaller for those salmon spending 1 or more years in fresh water than for those spending their first year in the sea (see Table I). For sockeye and coho examined and for those chinooks apparently spending 1 year in fresh water, the diameter of the first-year band[4] rarely exceeded 1.10 mm, whereas for pinks, chums, and for the other chinooks, diameters very rarely were less than 1.10 mm.

Among salmon spending their first year at sea, the average diameter of the first-year band for pinks was slightly less than that for chinooks and much smaller than that for chums (Table I).

(b) RETICULATION. Most circuli form continuous ridges only on the anterior part of the scale. In the area posterior from the focus, most circuli "break up" and in many individuals form contorted reticulations. In sockeye this reticulation is ladder-like in form (Fig. 2 and 7A). Most pink salmon scales also exhibit ladder-like reticulations (Fig. 3 and 7A), although in some, the reticulations are more globular in form (Fig. 7B). Globular reticulations are typical of chum salmon scales (Fig. 4 and 7C) and of those of some chinook salmon. In coho scales (Fig. 5) and in most chinook scales (Fig. 6) reticulation of any type is lacking. Data on the occurrence of reticulations of different types in samples of different species are summarized in Table II.

(c) NUMBER OF "COMPLETE" CIRCULI IN THE POSTERIOR HALF OF THE SCALE. In pink and chum salmon most of the circuli terminate abruptly as they pass into the posterior part of the scale; very few (almost always less than five — see Table II) form a complete unbroken circle around the focus of the scale. The number of such "complete" circuli (i.e. those forming complete unbroken circles) in sockeye scales is somewhat higher (2–9) and the number in chinook and coho scales higher still (3–13).

(d) NUMBER OF BROKEN CIRCULI IN THE POSTERIOR PART OF THE SCALE. In addition to the unbroken circuli mentioned above, there is a number of broken circuli which encircle the focus, especially in coho and chinook scales. Individual coho exhibited from 0 to 20 such circles of "broken" circuli, and chinooks from 0 to 18 (Table II). No sockeye, pinks, or chums had more than seven such broken circuli.

(e) NUMBER OF ANNULI. Virtually all pink salmon mature approximately 1½ years after emergence from the gravel and hence only a single annulus forms on their scales. Except for a few chums, virtually all other salmon return to spawn 2½ or more years after emergence, and more than one annulus forms on their scales. Thus among maturing salmon any individual exhibiting more than one annulus is almost certainly not a pink salmon.

---

[4]The diameter of the first-year band is measured along a line drawn through the focus at right angles to the longest axis of the scale (Fig. 1).

TABLE I. Diameter of first-year band of scales of salmon sampled in ...rcial

| Species | Area | Diameter of ... mm × | | |

rcial fishing areas along the British Columbia coast in 1963.

ter of	mm × 100)																													Total
5 160	185	190	195	200	205	210	215	220	225	230	235	240	245	250	255	260	265	270	275	280	285	290	295	300	305	310	315	320	
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	200
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	200
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	400
5 18	7	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	200
12	10	10	9	4	2	2	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	199
30	17	11	9	4	3	2	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	399
..	3	4	3	12	5	16	9	18	9	26	11	31	7	10	6	7	9	5	1	2	..	2	1	1	..	..	..	..	..	200
1	..	3	..	6	2	7	9	15	10	17	9	26	13	29	8	15	8	7	3	1	2	2	..	3	1	..	1	..	..	200
1	3	7	3	18	7	23	18	33	19	43	20	57	20	39	14	22	17	12	4	3	2	4	1	4	1	..	1	..	..	400
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	91
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	34
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	75
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	168
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	368
1	..	..	..	..	..	1	..	1	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	55
2	1	1	2	1	1	2	1	4	2	..	2	2	..	5	1	3	1	3	..	3	..	1	..	..	..	..	..	..	1	100
2	2	3	1	2	..	2	..	5	..	2	..	1	..	..	..	2	..	1	1	..	..	..	..	..	..	..	..	..	..	45
..	5	2	1	2	3	2	2	3	3	3	2	..	..	..	..	..	..	..	2	..	..	..	1	..	..	..	..	..	..	200
5	8	6	4	5	4	7	3	13	5	5	4	4	..	6	1	5	1	4	3	3	..	1	1	..	..	..	..	1		400
																														1,967

TABLE II. Frequency of occurrence of circulus reticulation of different types, and of the numbers of complete and broken circuli in the posterior part of the scales of Pacific salmon sampled in various fishing areas along the British Columbia coast in 1963 (see text).

Species	Area	Freshwater annulus		Reticulation[a]				Number of complete posterior circuli													Number of broken posterior circuli																					Total
		Present	Absent	A	L	G	L&G	0	1	2	3	4	5	6	7	8	9	10	11	12	13	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
								Numbers of fish														*Numbers of fish*																					
Sockeye	Fraser River	200	0	0	200	0	0	..	..	1	19	58	70	39	13	..	..	..	..	..	..	8	50	67	51	20	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	300
	Skeena River	200	0	0	200	0	0	..	..	1	9	43	65	52	22	6	2	..	..	..	..	7	43	62	55	29	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	200
Total		400	0	0	400	0	0	..	..	2	28	101	135	91	35	6	2	..	..	..	..	15	93	129	106	49	8	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	400
Pink	Skeena River	0	200	0	168	16	16	16	46	59	55	17	7	..	..	..	..	..	..	..	..	9	63	72	43	10	1	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	200
	Fraser River	0	199	0	166	8	25	16	86	68	21	7	1	..	..	..	..	..	..	..	..	4	48	83	50	12	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	199
Total		0	399	0	334	24	41	32	132	127	76	24	8	..	..	..	..	..	..	..	..	13	111	155	93	22	3	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	399
Chum	Skeena River	0	200	0	0	200	0	12	64	98	23	3	..	..	..	..	..	..	..	..	..	28	124	43	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	200
	Fraser River	0	200	0	0	200	0	7	95	88	10	..	..	..	..	..	..	..	..	..	..	25	127	42	5	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	200
Total		0	400	0	0	400	0	19	159	186	33	3	..	..	..	..	..	..	..	..	..	53	251	85	10	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	400
Coho	Skeena River	91	0	91	0	0	0	..	..	..	1	4	14	20	27	9	8	2	3	2	1	..	1	1	3	2	3	6	10	11	9	8	6	7	10	8	..	2	2	..	1	..	1	91
	Nass River	34	0	34	0	0	0	..	..	..	..	1	4	14	3	6	2	2	1	..	1	..	1	..	..	..	2	1	1	2	3	8	5	..	3	4	2	1	..	1	..	..	..	34
	Hecate Strait	75	0	73	0	2	0	..	..	..	..	4	8	17	10	12	8	4	7	4	1	..	..	..	1	6	1	7	4	5	6	19	5	7	8	2	2	1	..	1	..	..	..	75
	Fraser River	168	0	168	0	0	0	..	..	..	4	9	34	51	33	18	12	2	3	2	..	1	2	8	10	15	23	30	21	15	15	11	4	8	4	..	1	..	..	..	..	..	..	168
Total		368	0	366	0	2	0	..	..	..	5	18	60	102	73	45	30	10	14	8	3	1	4	9	14	23	29	44	36	33	33	46	20	22	25	14	5	4	2	2	1	..	1	368
Chinook	Skeena River	48	7	54	0	1	0	..	..	..	..	..	7	16	12	15	2	2	..	1	..	..	4	12	13	11	5	4	2	3	1	..	..	..	..	..	..	..	..	..	..	..	..	55
	Gulf of Georgia	50	50	93	0	7	0	..	..	..	..	2	4	10	24	28	14	11	6	1	..	2	8	11	25	28	11	3	7	4	..	..	1	..	..	..	..	..	..	..	..	..	..	100
	Hecate Strait	2	43	42	0	3	0	..	..	..	..	..	2	6	12	10	5	3	7	..	..	..	3	7	8	8	7	6	5	..	..	1	..	..	..	..	..	..	..	..	..	..	..	45
	Fraser River	161	39	116	0	84	0	1	..	9	8	18	45	55	35	17	8	4	..	..	..	..	..	..	4	7	13	25	36	31	30	17	17	15	2	1	1	..	..	1	..	..	..	200
Total		261	139	305	0	95	0	1	..	9	8	20	58	87	83	70	29	20	13	2	..	2	15	30	50	54	36	38	50	38	31	18	18	15	2	1	1	..	..	1	..	..	..	400
Grand Total																																											1,967

[a]Note: A — reticulation absent; L — ladder-like reticulation; G — globular reticulation; L&G — ladder-like and globular reticulation mixed.

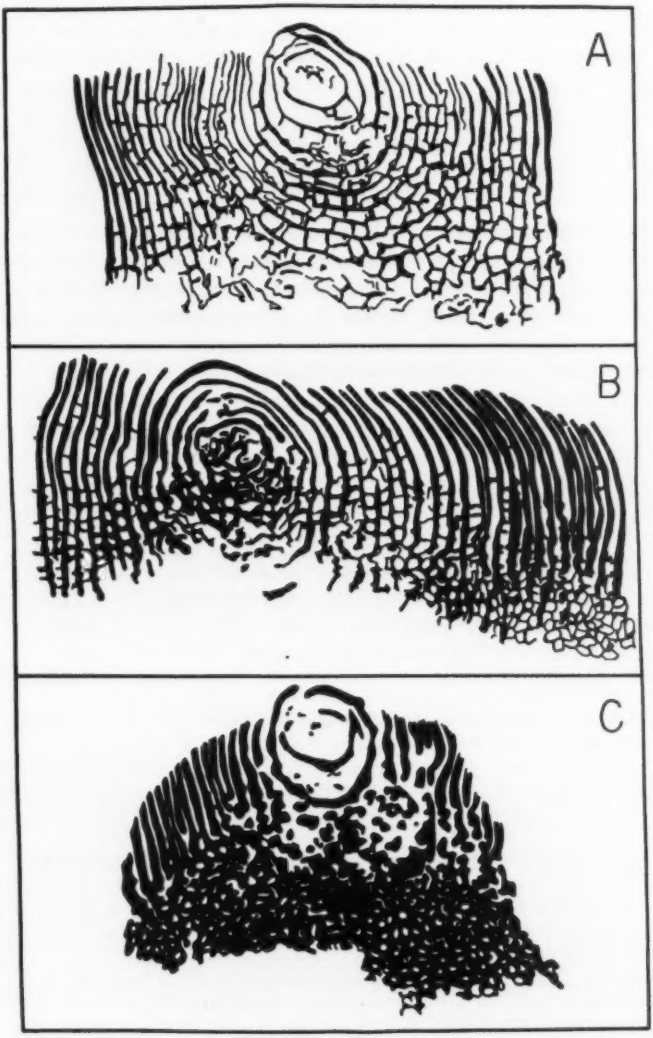


FIG. 7. Drawings of (A) ladder-like reticulation (present on all sockeye and most pink salmon scales); (B) mixed ladder-like and globular reticulation (present on some pink salmon scales); (C) globular reticulation (present on all species except sockeye).

ESTABLISHMENT OF THE KEY TO IDENTIFY SPECIES

On the basis of observed differences in scale characters the following key to the identification of the five North American species of Pacific salmon was derived. The key separates all samples into one of nine categories: five categories wherein the species could be identified precisely (those in which the fish were designated as being *only* one of sockeye, pink, chum, coho, or chinook) and four categories where it was not possible to identify the species precisely but where the assignment could be narrowed to one of two or three possibilities (*either* pink or chum, *either* chum or chinook, *either* coho or chinook, or *one* of pink, chum, or chinook.)

To use the key, the first numbered statement is considered with respect to the specimen at hand. If false, the unnumbered alternative statement immediately below the first statement is considered. If, on the other hand, the first statement is true, then the statement indicated by the number in brackets to the right is then considered. The process is repeated until a species name or species names occur at the end of the statement.

KEY TO THE IDENTIFICATION OF THE FIVE NORTH AMERICAN SPECIES OF PACIFIC SALMON (GENUS *ONCORHYNCHUS*)

1 At least one freshwater year band (circuli in the first-year band delicate in structure, very compactly spaced, diameter of the first-year band usually 1.10 mm or less).....(2)
– No freshwater year bands (circuli in the first-year band coarse in structure, widely spaced, diameter of the first-year band usually 1.11 mm or more).....(5)

2 Reticulation on the posterior edge of the scale always ladder-like.....sockeye (*O. nerka*)
– Reticulation on the posterior edge of the scale most often absent; if present, globular.....(3)

3 More than one ocean annulus.....chinook (*O. tshawytscha*)
– One ocean annulus only.....(4)

4 13 or more broken circuli in the posterior area of the scale.....coho (*O. kisutch*)
– 12 or less broken circuli in the posterior area of the scale.....coho or chinook (*O. kisutch* or *O. tshawytscha*)

5 Reticulation on the posterior edge of the scale absent.....chinook (*O. tshawytscha*)
– Reticulation on the posterior edge of the scale (a) ladder-like or (b) ladder-like and globular mixed or (c) globular.....(6)

6 Reticulation on the posterior edge of the scale (a) ladder-like or (b) ladder-like and globular mixed.....pink (*O. gorbuscha*)
– Reticulation on the posterior edge of the scale globular.....(7)

7 One ocean annulus only.....(8)
– More than one ocean annulus.....(10)

8 (a) eight or more broken and/or (b) six or more complete circuli in the posterior area of the scale.....chinook (*O. tshawytscha*)
– (a) one to seven broken and/or (b) three to five complete circuli in the posterior area of the scale.....chum or pink or chinook (*O. keta* or *O. gorbuscha* or *O. tshawytscha*)
– (a) broken circuli absent from posterior area of the scale and/or (b) two or less complete circuli in the posterior area of the scale.....pink or chum (*O. gorbuscha* or *O. keta*) (9)

9 Diameter of the first ocean year band 1.75 mm or less.....pink (*O. gorbuscha*)
– Diameter of the first ocean year band 2.11 mm or more.....chum (*O. keta*)
– Diameter of the first ocean year band ranging between 1.76 mm and 2.10 mm.....pink or chum (*O. gorbuscha* or *O. keta*)

10 (a) eight or more broken and/or (b) six or more complete circuli in the posterior area of the scale.....chinook (*O. tshawytscha*)
– (a) one to seven broken and/or (b) three to five complete circuli in the posterior area of the scale.....chum or chinook (*O. keta* or *O. tshawytscha*)
– (a) broken circuli absent from posterior area of the scale and/or (b) two or less complete circuli in the posterior area of the scale.....chum (*O. keta*)

Using the key, the standard samples involved in developing the key were processed as if they had been unknowns. As shown in Tables III and IV, the species was identified precisely for 100% of the sockeye, 98.5% of the pinks, 94.7% of the chums, 93.2% of the chinooks, and 14.7% of the coho. The remaining 1.5% of the pinks were individuals having scale characters similar to those of chums or chinooks exhibiting a single marine annulus (such one-annulus chums and chinooks occur only infrequently among mature salmon taken in coastal waters). The remaining 5.3% chums for which the species could not be determined precisely were individuals possessing the same type of reticulation as chinook salmon and could not be separated from the latter. The greatest difficulty in separation was experienced between coho and chinook, many of which have the same life-history pattern of spending 1 year in fresh water and 18 additional months in the sea before maturation and also have relatively similar reticulation and similar broken and complete posterior circuli patterns. A total of 6% of the chinooks examined, and 85.3% of the coho were 3_2 individuals which had scale patterns that resulted in their classification in the "coho or chinook" category.[5] None of the cohos was confused with any of the other three species, but three of the chinooks could not be separated from chums. Thus, the key provided precise identification of the species of well over 90% of the sockeye, pinks, chums, and chinooks. Only 14% of the cohos could be identified precisely. However, the remaining 86% of the cohos were separable from all other species except chinooks.

As a test of the effectiveness of the key, scales from a number of small samples of each species were examined from various coastal areas in British Columbia, southeastern, central, and western Alaska, the eastern coast of the USSR, and from Hokkaido in northern Japan. The results are given in Tables V to VIII. As shown in Table VII, all 243 of the sockeye were precisely identified. Of the 249 pinks sampled, scales provided precise identifications for 243 (97.6%). The remaining 6 (4 from the small Nushagak fishery in Bristol Bay, Alaska, and 2 from the Utoka River in Kamchatka) were incorrectly classified as chinooks because circuli reticulations were lacking from the posterior part of their scales. Of the 275 chums sampled, 266 (96.7%) were identified precisely on the basis of their scale patterns. An additional 2.5% keyed out into the mixed category "chum or chinook" and one from the Utoka River in Kamchatka

[5]In the present paper, the Gilbert (1913) system of age designation is used. Here, age refers to the year of life dating from time of egg deposition rather than the number of anniversaries passed. For example, a sockeye captured in the fishery during the summer of 1964 that had arisen from eggs deposited in the autumn of 1960 would be in its fourth year of life and would be called a 4-year-old (4) even though it had only passed three anniversaries since egg deposition. The year in which migration to sea took place is indicated by a subscript. Thus, if the fish spent 1 year in fresh water before migrating to sea in its second year, the age of the particular fish would be designated as 4_2.

ESTABLISHMENT OF THE KEY TO IDENTIFY SPECIES

On the basis of observed differences in scale characters the following key to the identification of the five North American species of Pacific salmon was derived. The key separates all samples into one of nine categories: five categories wherein the species could be identified precisely (those in which the fish were designated as being *only* one of sockeye, pink, chum, coho, or chinook) and four categories where it was not possible to identify the species precisely but where the assignment could be narrowed to one of two or three possibilities (*either* pink or chum, *either* chum or chinook, *either* coho or chinook, or *one* of pink, chum, or chinook.)

To use the key, the first numbered statement is considered with respect to the specimen at hand. If false, the unnumbered alternative statement immediately below the first statement is considered. If, on the other hand, the first statement is true, then the statement indicated by the number in brackets to the right is then considered. The process is repeated until a species name or species names occur at the end of the statement.

KEY TO THE IDENTIFICATION OF THE FIVE NORTH AMERICAN SPECIES OF PACIFIC SALMON (GENUS *ONCORHYNCHUS*)

1 At least one freshwater year band (circuli in the first-year band delicate in structure, very compactly spaced, diameter of the first-year band usually 1.10 mm or less) ..... (2)
– No freshwater year bands (circuli in the first-year band coarse in structure, widely spaced, diameter of the first-year band usually 1.11 mm or more) ..... (5)

2 Reticulation on the posterior edge of the scale always ladder-like ..... sockeye (*O. nerka*)
– Reticulation on the posterior edge of the scale most often absent; if present, globular ..... (3)

3 More than one ocean annulus ..... chinook (*O. tshawytscha*)
– One ocean annulus only ..... (4)

4 13 or more broken circuli in the posterior area of the scale ..... coho (*O. kisutch*)
– 12 or less broken circuli in the posterior area of the scale ..... coho or chinook (*O. kisutch* or *O. tshawytscha*)

5 Reticulation on the posterior edge of the scale absent ..... chinook (*O. tshawytscha*)
– Reticulation on the posterior edge of the scale (a) ladder-like or (b) ladder-like and globular mixed or (c) globular ..... (6)

6 Reticulation on the posterior edge of the scale (a) ladder-like or (b) ladder-like and globular mixed ..... pink (*O. gorbuscha*)
– Reticulation on the posterior edge of the scale globular ..... (7)

7 One ocean annulus only ..... (8)
– More than one ocean annulus ..... (10)

8 (a) eight or more broken and/or (b) six or more complete circuli in the posterior area of the scale ..... chinook (*O. tshawytscha*)
– (a) one to seven broken and/or (b) three to five complete circuli in the posterior area of the scale ..... chum or pink or chinook (*O. keta* or *O. gorbuscha* or *O. tshawytscha*)
– (a) broken circuli absent from posterior area of the scale and/or (b) two or less complete circuli in the posterior area of the scale ..... pink or chum (*O. gorbuscha* or *O. keta*) (9)

9 Diameter of the first ocean year band 1.75 mm or less ..... pink (*O. gorbuscha*)
– Diameter of the first ocean year band 2.11 mm or more ..... chum (*O. keta*)
– Diameter of the first ocean year band ranging between 1.76 mm and 2.10 mm ..... pink or chum (*O. gorbuscha* or *O. keta*)

10 (a) eight or more broken and/or (b) six or more complete circuli in the posterior area of the scale.....chinook (*O. tshawytscha*)
– (a) one to seven broken and/or (b) three to five complete circuli in the posterior area of the scale.....chum or chinook (*O. keta* or *O. tshawytscha*)
– (a) broken circuli absent from posterior area of the scale and/or (b) two or less complete circuli in the posterior area of the scale.....chum (*O. keta*)

Using the key, the standard samples involved in developing the key were processed as if they had been unknowns. As shown in Tables III and IV, the species was identified precisely for 100% of the sockeye, 98.5% of the pinks, 94.7% of the chums, 93.2% of the chinooks, and 14.7% of the coho. The remaining 1.5% of the pinks were individuals having scale characters similar to those of chums or chinooks exhibiting a single marine annulus (such one-annulus chums and chinooks occur only infrequently among mature salmon taken in coastal waters). The remaining 5.3% chums for which the species could not be determined precisely were individuals possessing the same type of reticulation as chinook salmon and could not be separated from the latter. The greatest difficulty in separation was experienced between coho and chinook, many of which have the same life-history pattern of spending 1 year in fresh water and 18 additional months in the sea before maturation and also have relatively similar reticulation and similar broken and complete posterior circuli patterns. A total of 6% of the chinooks examined, and 85.3% of the coho were 3_2 individuals which had scale patterns that resulted in their classification in the "coho or chinook" category.[5] None of the cohos was confused with any of the other three species, but three of the chinooks could not be separated from chums. Thus, the key provided precise identification of the species of well over 90% of the sockeye, pinks, chums, and chinooks. Only 14% of the cohos could be identified precisely. However, the remaining 86% of the cohos were separable from all other species except chinooks.

As a test of the effectiveness of the key, scales from a number of small samples of each species were examined from various coastal areas in British Columbia, southeastern, central, and western Alaska, the eastern coast of the USSR, and from Hokkaido in northern Japan. The results are given in Tables V to VIII. As shown in Table VII, all 243 of the sockeye were precisely identified. Of the 249 pinks sampled, scales provided precise identifications for 243 (97.6%). The remaining 6 (4 from the small Nushagak fishery in Bristol Bay, Alaska, and 2 from the Utoka River in Kamchatka) were incorrectly classified as chinooks because circuli reticulations were lacking from the posterior part of their scales. Of the 275 chums sampled, 266 (96.7%) were identified precisely on the basis of their scale patterns. An additional 2.5% keyed out into the mixed category "chum or chinook" and one from the Utoka River in Kamchatka

[5]In the present paper, the Gilbert (1913) system of age designation is used. Here, age refers to the year of life dating from time of egg deposition rather than the number of anniversaries passed. For example, a sockeye captured in the fishery during the summer of 1964 that had arisen from eggs deposited in the autumn of 1960 would be in its fourth year of life and would be called a 4-year-old (4) even though it had only passed three anniversaries since egg deposition. The year in which migration to sea took place is indicated by a subscript. Thus, if the fish spent 1 year in fresh water before migrating to sea in its second year, the age of the particular fish would be designated as 4_2.

TABLE III. Results of processing through the key "standard" samples of salmon of different ages sampled along the British Columbia coast in 1963. Table indicates number of cases where correct and precise classifications were achieved and number of cases where assignment to "mixed" categories only was possible.

Species	Area	Correct and precise classifications											Classifications into mixed categories[a]										Total no. of samples
		2_1	3_1	4_1	5_1	3_2	4_2	5_2	6_2	4_3	5_3	6_3	2_1	3_1	4_1	5_1	3_2	4_2	5_2	6_2	4_3	5_3	6_3	
		Numbers of fish											*Numbers of fish*										
Sockeye	Skeena R.	..	..	..	..	10	130	49	..	..	9	2	..	..	..	..	0	0	0	..	..	0	0	200
	Fraser R.	..	..	..	..	..	193	..	..	..	7	..	..	..	..	..	..	0	..	..	..	0	..	200
	Total	..	..	..	..	10	323	49	..	..	16	2	..	..	..	..	0	0	0	..	..	0	0	400
Pink	Skeena R.	196	..	..	..	..	..	..	..	..	..	..	4 Pi-Ch-Ck	..	..	..	..	..	..	..	..	..	..	200
	Fraser R.	197	..	..	..	..	..	..	..	..	..	..	1 Pi-Ch-Ck 1 Pi-Ch	..	..	..	..	..	..	..	..	..	..	199
	Total	393	..	..	..	..	..	..	..	..	..	..	6	..	..	..	..	..	..	..	..	..	..	399
Chum	Skeena R.	..	86	93	5	..	..	..	..	..	..	..	..	6 Ch-Ck	10 Ch-Ck	0	..	..	..	..	..	..	..	200
	Fraser R.	..	66	129	..	..	..	..	..	..	..	..	..	3 Ch-Ck	2 Ch-Ck	0	..	..	..	..	..	..	..	200
	Total	..	152	222	5	..	..	..	..	..	..	..	..	9	12	..	..	..	..	..	..	..	..	400
Coho	Skeena R.	..	..	..	..	24	..	..	..	..	..	..	..	..	..	..	67 Co-Ck	..	..	..	..	..	..	91
	Nass R.	..	..	..	..	11	..	..	..	..	..	..	..	..	..	..	23 Co-Ck	..	..	..	..	..	..	34
	Hecate St.	..	..	..	..	14	..	..	..	..	..	..	..	..	..	..	60 Co-Ck	..	..	..	1 Co-Ck	..	..	75
	Fraser R.	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..	163 Co-Ck	..	..	..	..	..	..	168
	Total	..	..	..	..	54	..	..	..	..	..	..	..	..	..	..	313	..	..	..	1	..	..	368
Chinook	Skeena R.	..	5	2	..	..	24	13	..	..	..	..	..	..	..	..	11 Co-Ck	..	..	..	..	..	..	55
	St. Georgia	..	23	24	3	..	18	20	..	..	..	..	..	..	..	..	12 Co-Ck	..	..	..	..	..	..	100
	Hecate St.	..	20	22	1	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	45
	Fraser R.	..	17	18	..	1	113	46	1	..	..	..	..	2 Ch-Ck	1 Ch-Ck	..	1 Co-Ck	..	..	..	..	..	..	200
	Total	..	65	66	4	1	156	80	1	..	..	..	..	2	1	..	24	..	..	..	..	..	..	400

Note: Pi-Ch — pink or chum; Pi-Ch-Ck — pink or chum or chinook; Ch-Ck — chum or chinook; Co-Ck — coho or chinook

Total	..	65	66	4	1	156	80	1	..	..	..	..	2	1	..	24	..	..	..	..	..	400

Note: Pi-Ch — pink or chum; Pi-Ch-Ch — pink or chum or chinook; Ch-Ch — chum or chinook; Co-Ch — coho or chinook

TABLE IV. Summary of results of processing through the key "standard" samples of salmon sampled along the British Columbia coast in 1963. Table shows numbers and percentages of individuals classified into various species categories.

Species		Category									Total
		Sockeye	Pink	Chum	Coho	Chinook	Pink or Chum	Pink, Chum or Chinook	Chum or Chinook	Coho or Chinook	
Sockeye	No.	400	0	0	0	0	0	0	0	0	400
	%	100.0	0	0	0	0	0	0	0	0	100.0
Pink	No.	0	393	0	0	0	1	5	0	0	399
	%	0	98.5	0	0	0	0.2	1.3	0	0	100.0
Chum	No.	0	0	379	0	0	0	0	21	0	400
	%	0	0	94.7	0	0	0	0	5.3	0	100.0
Coho	No.	0	0	0	54	0	0	0	0	314	368
	%	0	0	0	14.7	0	0	0	0	85.3	100.0
Chinook	No.	0	0	0	0	373	0	0	3	24	400
	%	0	0	0	0	93.2	0	0	0.8	6.0	100.0

TABLE V. Diameter of first year band of scales of salmon sampled in various com

Species	Area	Year	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	12
Sockeye	*British Columbia*																				
	Rivers Inlet	1963	2	1	7	9	2	2	..	2	..	..	..	..	..	..	..	..	..	..	..
	Alaska																				
	Snettisham	1963	..	2	2	11	5	3	1	..	1	..	..	..	..	..	..	..	..	..	..
	Cook Inlet	1956	..	..	..	1	6	2	3	8	2	2	..	1	..	..	..	..	..	..	..
	Igulgig River	1963	..	..	..	..	1	..	2	4	8	7	2	1	..	..	..	..	..	..	..
	Egegik River	1963	..	..	..	..	3	2	4	2	3	1	..	2	..	..	..	..	..	..	..
	Igushik River	1963	..	1	2	2	5	4	6	1	2	2	..	..	..	..	..	..	..	..	..
	Ugashik River	1963	..	2	6	5	4	2	1	1	2	2	..	..	..	..	..	..	..	..	..
	Togiak River	1963	..	..	..	..	..	..	8	8	3	3	2	1	..	..	..	..	..	..	..
	USSR																				
	Bilijinyaya River	1958	..	..	..	1	1	5	2	5	3	2	3	2	1	1	..	..	..	..	..
	Bolshaya River	1958	..	..	2	5	8	8	1	..	..	1	..	..	..	..	..	..	..	..	..
	Total		2	6	19	34	35	28	28	31	24	20	7	7	1	1	..	..	..	..	..
Chum	*Alaska*																				
	Ketchikan (Anan Bay)	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Petersburg (King Salmon Bay)	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Yakutat (Alsek River)	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Seldovia (Kalgin Island)	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Kodiak (Uyak Bay)	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Kodiak (Larsen Bay)	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Alaska Pen. (Shumagin Island)	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Bethel (Kuskokwim River)	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Yukon River (Alakanuk)	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	USSR																				
	Kamchatka River	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Kamchatka (Utoka River)	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Total		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Pink	*British Columbia*																				
	Nass River	1962	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3
	Alaska																				
	Cook Inlet (Kenai River)	1962	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
	Kariuk Lagoon	1962	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	7
	Unalaska Island	1962	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	6
	Kodiak (Uyak Bay)	1956	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3
	Bristol Bay (Nushagak Fishery)	1962	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Unalakleet River	1956	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2
	Yukon River (Old Andreafsky)	1956	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3
	USSR																				
	Utoka River	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3
	Amur River	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5
	Japan																				
	Hokkaido Island (Tokoro River)	1958	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Total		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	1	39
Coho	*Alaska*																				
	Trout Creek	1956	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	1	2	..	..
	Copper River	1959	..	..	..	..	..	1	..	3	6	7	3	4	2	1	2	1	..	..	..
	Attu (Lake Nicholas)	1956	..	..	..	..	..	..	..	1	3	2	2	2	1	3	..	1	1	..	..
	Attu (Gravel Pit)	1956	..	..	..	..	..	..	..	..	..	3	2	..	1	..	..	..	..	..	..
	Attu	1956	..	..	..	..	1	1	..	3	1	..	..	2	..	2	..	..	..	..	..
	Adak Island	1956	..	..	..	..	..	..	..	..	1	2	1	..	1	..	..	..	..	..	..
	Yukon River (Sunshine Bay)	1956	..	..	..	..	..	1	..	1	2	..	..	..	..	..	..	..	..	..	..
	Yukon River (Old Andreafsky)	1956	..	..	..	..	..	1	1	2	4	..	1	..	1	1	..	..	..	..	..
	Yukon River (Alakanuk)	1956	..	..	..	..	..	2	1	2	..	..	..	1	..	..	..	..	..	..	..
	Nome River	1956	..	..	..	..	2	2	2	2	3	1	2	1	..	1	..	1	..	..	..
	USSR																				
	Kamchatka	1958	..	..	1	1	4	7	2	5	5	..	3	1	..	1	..	..	..	..	..
	Kamchatka (Bolshaya River)	1958	..	..	..	3	3	6	3	3	8	3	1	..	..	..	..	..	..	..	..
	Kukhtui River	1958	..	..	..	..	1	4	2	3	9	3	2	..	2	..	1	..	..	1	..
	Total		..	..	1	4	11	25	11	25	43	22	17	11	8	9	3	4	3	1	..
Chinook	*Alaska*																				
	Bethel (Kuskokwim River)	1956	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
	Alakanuk River	1956	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Yukon River (Sunshine Bay)	1956	..	..	..	..	..	1	2	1	..	..	..	..	..	..	..	..	..	..	..
	Unalakleet River	1956	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Total		..	..	..	..	..	2	2	1	..	..	..	..	..	..	..	..	..	..	..

[a]Note: diameter of the first year band is measured along a line drawn through the focus at right angles to the longest axis of the scale.

areas along the British Columbian, Alaskan, and Asian coasts from 1956 to 1963.

of first-year band (mm × 100)*																																		Total No. samples
0	155	160	165	170	175	180	185	190	195	200	205	210	215	220	225	230	235	240	245	250	255	260	265	270	275	280	285	290	295	300				
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				17
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				26
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				243
..	..	..	..	..	2	1	..	..	3	4	2	1	4	4	1	1	..	1	1	..	..	..	..	..	..	..	..	..	..	..				25
..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	2	..	1	3	4	4	2	1	1	..	2	1	1	..	1	1				25
..	..	..	..	..	..	..	..	..	1	..	1	..	1	1	2	1	4	..	1	2	2	2	2	3	1	..	..	1	..	..				25
..	..	..	..	..	..	..	..	..	1	2	1	1	2	1	1	5	1	5	1	2	1	..	..	1	..	..	..	..	..	..				25
..	..	..	..	..	..	..	..	..	..	1	..	..	..	2	1	3	2	5	2	2	1	1	..	2	1	1	1	..	..	..				25
..	..	..	..	..	..	..	..	..	..	..	1	..	..	2	3	2	1	2	1	1	3	2	3	1	..	..	1	1	1	..				25
..	..	..	..	..	..	..	..	..	..	..	1	1	1	..	1	2	5	1	3	1	3	1	1	1	1	..	1	..	..	..				25
..	..	..	..	..	..	..	..	..	..	..	1	2	..	2	2	4	4	5	..	3	1	1	..	..	..	..	..	..	..	..				25
..	..	..	..	..	..	..	..	..	..	2	..	..	..	4	3	3	2	..	2	2	1	1	2	1	..	1	1	..	..	..				25
..	..	2	..	2	..	..	2	1	1	2	4	1	3	1	..	..	1	..	2	2	..	..	1	..	..	..	..	..	..	..				25
..	..	..	..	1	1	..	..	4	1	1	2	1	..	1	1	2	2	..	2	3	..	..	2	..	1	..	..	..	..	..				25
..	..	2	..	3	3	1	2	5	7	12	13	7	12	18	17	23	23	23	19	22	14	9	12	9	6	3	5	2	2	1				275
3	4	2	6	1	2	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
1	2	4	5	2	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				26
7	1	2	2	3	2	2	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
6	4	1	..	5	2	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
1	5	8	1	3	4	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				34
1	6	4	5	2	1	1	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				3
3	..	3	..	..	1	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				11
2	1	2	3	3	3	3	1	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
3	1	6	5	..	2	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				25
..	4	4	2	2	4	1	2	2	1	..	..	..	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..				25
23	27	36	29	21	21	13	8	6	3	1	..	1	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..				249
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				5
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				30
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				16
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				6
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				10
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				5
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				4
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				11
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				6
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				17
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				30
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				30
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				28
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..				198
..	..	..	..	..	..	..	1	1	..	3	10	3	5	10	2	9	2	3	8	8	4	1	2	3	1	1	1	..	1	..				80
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	1	..	..	..	..	1	1	..	..	..	..	..	..	..	..				4
..	..	..	..	..	..	..	..	..	1	..	..	1	..	1	..	..	1	..	2	1	..	..	..	..	..	1	..	..	..	..				12
..	..	..	..	..	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	1	..	..	..	..				5
..	..	..	..	1	..	1	2	1	3	10	4	5	11	3	10	3	3	10	9	5	2	4	3	1	3	1	..	1	..				101

TABLE VI. [Frequency of occurrence of circulus reticulation of different types, and of the numbers of com circul the British Columbian, Al coasts

Species	Area and year		Freshwater annulus		Reticulation*				Number of complete posterior c								13	0
			Present	Absent	A	L	G	L&G	0	1	2	3	4	5	6	7		
									Numbers of fish									
Sockeye	*British Columbia*																	
	Rivers Inlet	1963	25	0	0	25	0	0	..	..	2	3	8	5	5	1	..	
	Alaska																	
	Snettisham	1963	25	0	0	25	0	0	..	..	..	2	7	6	5	5	..	
	Cook Inlet	1956	25	0	0	25	0	0	..	..	1	3	6	9	1	5	..	
	Iguigig River	1963	25	0	0	25	0	0	..	..	..	5	12	5	3	..	..	
	Egegik River	1963	17	0	0	17	0	0	..	2	..	7	5	2	1	..	..	
	Igushik River	1963	25	0	0	25	0	0	..	..	2	8	11	3	1	..	..	
	Ugashik River	1963	25	0	0	25	0	0	..	..	2	12	6	5	..	..	..	
	Togiak River	1963	25	0	0	25	0	0	..	..	5	2	14	4	..	..	..	
	USSR																	
	Biljinyaya River	1958	26	0	0	26	0	0	..	..	..	4	8	6	7	1	..	
	Bolshaya River	1958	25	0	0	25	0	0	..	..	1	..	12	6	6	..	..	
Total			243	0	0	243	0	0	..	2	13	46	89	51	29	12	..	
Chum	*Alaska*																	
	Ketchikan (Anan Bay)	1958	0	25	0	0	25	0	19	5	1	..	..	..	..	..	..	
	Petersburg (King Salmon Bay)	1958	0	25	0	0	25	0	19	5	1	..	..	..	..	..	..	
	Yakutat (Aiwek River)	1958	0	25	0	0	25	0	17	6	2	..	..	..	..	..	..	
	Seldovia (Kalgin Island)	1958	0	25	0	0	25	0	10	7	6	1	1	..	..	..	..	
	Kodiak (Uyak Bay)	1958	0	25	0	0	25	0	18	6	1	..	..	..	..	..	..	
	Kodiak (Larsen Bay)	1958	0	25	0	0	25	0	13	5	3	3	..	..	1	..	..	
	Alaska Pen. (Shumagin Island)	1958	0	25	0	0	25	0	16	7	2	..	..	..	..	..	..	
	Bethel (Kuskokwim River)	1958	0	25	0	0	25	0	15	8	2	..	..	..	..	..	..	
	Yukon River (Alakanuk)	1958	0	25	0	0	25	0	16	7	2	..	..	..	..	..	..	
	USSR																	
	Kamchatka River	1958	0	25	0	0	25	0	4	6	9	5	1	..	..	..	..	
	Kamchatka (Utoka River)	1958	0	25	0	0	25	0	16	6	2	1	..	..	..	..	..	
Total			0	275	0	0	275	0	163	68	31	10	2	..	1	..	..	
Pink	*British Columbia*																	
	Nass River	1962	0	25	0	21	0	4	18	4	2	..	1	..	..	..	..	
	Alaska																	
	Cook Inlet (Kenai River)	1962	0	26	0	25	0	1	21	3	2	..	..	..	..	..	..	
	Kariuk Lagoon	1962	0	25	0	25	0	0	20	2	3	..	..	..	..	..	..	
	Unalaska Island	1962	0	25	0	25	0	3	25	..	..	..	..	..	..	..	..	
	Kodiak (Uyak Bay)	1956	0	34	0	22	0	12	29	3	2	..	..	..	..	..	..	
	Bristol Bay (Nushagak Fishery)	1962	0	25	4	17	0	4	25	..	..	..	..	..	..	..	..	
	Unalakleet River	1956	0	3	0	2	0	1	3	..	..	..	..	..	..	..	..	
	Yukon River (Old Andreafsky)	1956	0	11	0	9	0	2	10	1	..	..	..	..	..	..	..	
	USSR																	
	Utoka River	1958	0	25	2	19	0	4	16	5	4	..	..	..	..	..	..	
	Amur River	1958	0	25	0	20	0	5	19	6	..	..	..	..	..	..	..	
	Japan																	
	Hokkaido Island (Tokoro River)	1958	0	25	0	16	0	9	24	1	..	..	..	..	..	..	..	
Total			0	249	6	198	0	45	210	25	13	..	1	..	..	..	..	
Coho	*Alaska*																	
	Trout Creek	1956	5	0	4	0	1	0	..	..	1	1	1	1	1	..	..	
	Copper River	1959	30	0	26	0	4	0	..	1	3	8	5	9	3	1	..	
	Attu (Lake Nicholas)	1956	16	0	7	0	9	0	2	..	1	4	1	..	2	4	..	
	Attu (Gravel Pit)	1956	6	0	4	0	2	0	1	..	1	..	1	1	..	2	..	
	Attu	1956	10	0	2	0	8	0	..	1	..	1	1	2	2	1	..	
	Adak Island	1956	5	0	3	0	2	0	..	..	..	..	1	4	..	..	..	
	Yukon River (Sunshine Bay)	1956	4	0	4	0	0	0	..	..	..	1	..	1	..	1	..	
	Yukon River (Old Andreafsky)	1956	11	0	10	0	1	0	..	..	1	2	1	5	2	..	..	
	Yukon River (Alakanuk)	1956	6	0	5	0	1	0	..	..	..	3	2	1	..	..	..	
	Nome River	1956	17	0	12	0	5	0	..	..	..	..	2	2	2	6	..	
	USSR																	
	Kamchatka	1958	30	0	26	0	4	0	2	..	3	5	6	2	2	3	..	
	Kamchatka (Bolshaya River)	1958	30	0	26	0	4	0	1	2	4	3	6	5	5	2	..	1
	Kukhtui River	1958	28	0	26	0	2	0	1	..	2	4	12	1	6	..	..	
Total			198	0	155	0	43	0	7	4	16	32	39	34	25	20	..	1
Chinook	*Alaska*																	
	Bethel (Kuskokwim River)	1956	2	78	64	0	16	0	23	17	15	9	8	6	2	..	..	
	Alakanuk River	1956	0	4	4	0	0	0	..	1	2	..	..	1	..	..	..	
	Yukon River (Sunshine Bay)	1956	4	8	9	0	3	0	4	1	1	4	2	..	..	..	..	
	Unalakleet River	1956	0	5	4	0	1	0	..	..	5	..	..	..	..	..	..	
Total			6	95	81	0	20	0	27	19	23	13	10	7	2	..	..	

*Note: A — Reticulation absent; L — Ladder-like reticulation; G — Globular reticulation; L&G — Ladder-like and globular reticul

circuli in the posterior part of the scales of Pacific salmon sampled in various commercial fishing areas along coasts from 1956 to 1963.

	Number of broken posterior circuli																										Total No. samples
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
	Numbers of fish																											
	1	3	4	4	5	3	2	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	1	6	12	6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	1	2	7	4	2	6	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	..	8	14	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	..	3	1	7	3	1	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	17
	..	..	1	6	5	5	4	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	..	1	6	5	3	7	2	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	2	2	3	11	3	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	..	1	3	5	8	1	6	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	26
	..	..	2	7	7	5	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	1	7	30	63	57	33	26	20	3	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	343
	..	3	2	7	5	6	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	1	1	7	11	1	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	1	..	3	5	8	3	3	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	3	4	4	6	5	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	..	4	8	6	5	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	2	1	6	7	3	4	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	..	9	4	6	4	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	4	7	7	5	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	3	10	8	..	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	3	6	9	3	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	3	10	6	5	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	7	24	71	70	48	33	18	3	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	275
	..	..	2	3	2	8	6	2	..	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	2	5	6	5	7	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	26
	..	..	2	2	5	7	7	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	1	3	4	6	3	4	1	2	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	1	5	7	3	10	1	3	1	1	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	34
	7	11	7	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	..	..	1	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3
	1	2	2	..	1	..	3	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	11
	..	..	..	3	5	6	5	3	1	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	..	..	..	5	3	2	4	3	3	2	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	2	8	3	2	6	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
	11	27	30	35	35	46	29	16	5	7	5	1	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	249
	..	..	..	..	..	..	..	..	..	..	1	1	1	..	..	1	..	..	..	1	..	..	..	..	..	..	..	5
1	..	..	..	..	..	..	..	..	..	1	1	3	2	3	3	2	4	3	1	2	3	1	..	1	..	..	..	30
4	..	..	..	..	..	..	..	1	..	..	1	2	1	1	1	..	1	..	1	2	1	1	..	..	1	1	1	16
2	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	1	1	..	..	..	..	1	2	..	..	..	6
1	..	..	..	..	..	1	1	..	..	..	1	..	..	..	..	..	1	3	2	..	..	..	..	1	..	..	..	10
..	..	..	..	..	..	..	1	..	2	..	..	..	..	..	..	..	1	..	..	1	..	..	..	..	..	..	..	5
1	..	..	..	..	..	..	..	..	..	1	..	1	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	4
..	..	..	..	..	..	..	..	..	..	1	2	3	2	1	2	..	..	..	..	..	..	..	..	..	..	..	..	11
..	..	..	..	..	..	..	..	..	..	..	..	..	1	1	1	1	2	..	..	..	..	..	..	..	..	..	..	6
6	..	..	..	..	..	..	..	..	1	..	3	2	5	2	3	..	..	..	..	1	..	..	..	..	..	..	..	17
3	..	..	..	..	..	1	..	..	..	..	..	2	3	..	3	1	1	2	1	5	5	3	..	1	..	1	1	30
2	1	..	..	..	..	..	1	1	..	1	1	4	4	2	2	5	1	1	1	..	3	1	..	..	..	1	1	30
..	..	..	..	..	1	..	..	..	3	..	..	2	1	1	2	5	1	3	3	2	2	1	1	..	..	..	..	28
20	1	..	..	..	..	1	2	3	2	7	4	10	20	20	11	17	17	14	14	7	14	14	7	2	5	1	3	3	198
..	..	..	..	1	3	3	11	9	10	7	12	6	6	4	4	1	2	1	..	..	..	..	..	..	..	..	..	..	80
..	..	..	..	..	..	..	2	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4
..	..	..	..	..	1	..	1	1	3	2	1	2	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	12
..	..	..	..	1	1	1	..	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5
..	..	..	1	4	5	14	10	12	11	14	9	8	4	4	2	2	1	..	..	..	..	..	..	..	..	..	..	..	101

TABLE VII. Results of processing through the key samples of salmon of different ages [illegible] 1956 to 1963. Table indicates number of cases where correct and precise classificati[illegible], th[illegible] numb[illegible] class

Species	Area	Year	Correct and precise classificati[illegible]								N[illegible]
			2_1	3_1	4_1	5_1	6_1	2_2	3_2	4_2	
Sockeye	*British Columbia*										
	Rivers Inlet	1963	..	..	..	..	..	..	..	13	..
	Alaska										
	Snettisham	1963	..	..	..	..	..	..	..	3	..
	Cook Inlet	1956	..	..	..	..	..	..	..	5	..
	Iguigig River	1963	..	..	..	..	..	..	..	19	1
	Egegik River	1963	..	..	..	..	..	..	..	3	6
	Igushik River	1963	..	..	..	..	..	..	..	20	..
	Ugashik River	1963	..	..	..	..	..	..	..	5	1
	Togiak River	1963	..	..	..	..	..	..	..	17	..
	USSR										
	Blijinyaya River	1958	..	..	..	..	..	..	1	14	..
	Bolshaya River	1958	..	..	..	..	..	..	..	..	..
	Total		..	..	..	..	..	..	1	104	8
Chum	*Alaska*										
	Ketchikan (Anan Bay)	1958	..	..	17	8	..	..	..	..	..
	Petersburg (King Salmon Bay)	1958	..	1	19	5	..	..	..	..	..
	Yakutat (Alsek River)	1958	..	7	17	1	..	..	..	..	..
	Seldovia (Kalgin Island)	1958	..	7	14	2	..	..	..	..	..
	Kodiak (Uyak Bay)	1958	..	5	9	11	..	..	..	..	..
	Kodiak (Larsen Bay)	1958	..	5	7	9	..	..	..	..	..
	Alaska Pen. (Shumagin Island)	1958	..	11	12	2	..	..	..	..	..
	Bethel (Kuskokwim River)	1958	..	21	3	1	..	..	..	..	..
	Yukon River (Alakanuk)	1958	..	14	11	..	..	..	..	..	..
	USSR										
	Kamchatka River	1958	..	2	19	2	..	..	..	..	..
	Kamchatka (Utoka River)	1958	..	3	13	8	..	..	..	..	..
	Total		..	76	141	49	..	..	..	..	..
Pink	*British Columbia*										
	Nass River	1962	25	..	..	..	..	..	..	..	..
	Alaska										
	Cook Inlet (Kenai River)	1962	26	..	..	..	..	..	..	..	..
	Kariuk Lagoon	1962	25	..	..	..	..	..	..	..	..
	Unalaska Island	1962	25	..	..	..	..	..	..	..	..
	Kodiak (Uyak Bay)	1956	34	..	..	..	..	..	..	..	..
	Bristol Bay (Nushagak Fishery)	1962	21	..	..	..	..	..	..	..	..
	Unalakleet River	1956	3	..	..	..	..	..	..	..	..
	Yukon River (Old Andreafsky)	1956	11	..	..	..	..	..	..	..	..
	USSR										
	Utoka River	1958	23	..	..	..	..	..	..	..	..
	Amur River	1958	25	..	..	..	..	..	..	..	..
	Japan										
	Hokkaido Island (Tokoro River)	1958	25	..	..	..	..	..	..	..	..
	Total		243	..	..	..	..	..	..	..	..
Coho	*Alaska*										
	Trout Creek	1956	..	..	..	..	..	0	2	..	..
	Copper River	1959	..	..	..	..	..	..	23	..	..
	Attu (Lake Nicholas)	1956	..	..	..	..	..	..	10	..	..
	Attu (Gravel Pit)	1956	..	..	..	..	..	..	5	..	..
	Attu	1956	..	..	..	..	..	..	7	..	..
	Adak Island	1956	..	..	..	..	..	..	2	..	..
	Yukon River (Sunshine Bay)	1956	..	..	..	..	..	..	2	..	..
	Yukon River (Old Andreafsky)	1956	..	..	..	..	..	..	3	..	..
	Yukon River (Alakanuk)	1956	..	..	..	..	..	..	5	..	..
	Nome River	1956	..	..	..	..	..	..	6	..	..
	USSR										
	Kamchatka	1958	..	..	..	..	..	..	34	..	..
	Kamchatka (Bolshaya River)	1958	..	..	..	..	..	..	19	..	..
	Kukhtui River	1958	..	..	..	..	..	..	21	..	..
	Total		..	..	..	..	..	0	129	..	..
Chinook	*Alaska*										
	Bethel (Kuskokwim River)	1956	..	4	30	37	1	..	..	..	..
	Alakanuk River	1956	..	..	1	3	..	..	..	..	..
	Yukon River (Sunshine Bay)	1956	..	..	2	5	..	..	..	..	..
	Unakakleet River	1956	..	3	..	2	..	..	..	..	..
	Total		..	7	33	47	1	..	..	..	..

*Note: Ch — chinook; Co-Ck — coho or chinook; Ch-Ck — chum or chinook.

t ages
ificati
numb

us commercial fishing areas along the British Columbian, Alaskan and Asian coasts from
d, the number of cases where assignment to "mixed" categories only was possible, and the
classified.

							Classifications into mixed categories and misclassifications[a]											
			2_1	3_1	4_1	5_1	6_1	2_2	3_2	4_2	5_2	6_2	4_3	5_3	6_3	Total
			Numbers of fish													
..	19	..	..	..	..	..	..	..	..	0	0	..	..	..	..	25
..	3	..	..	..	..	..	..	..	..	0	0	..	..	..	..	25
..	5	..	..	..	..	..	..	..	..	0	0	..	..	..	..	25
..	10	1	..	..	..	..	..	..	..	0	0	..	..	0	0	25
..	2	6	..	..	..	..	..	..	..	0	..	..	..	0	0	17
..	20	..	..	..	..	..	..	..	..	0	0	..	..	0	..	25
..	5	1	..	..	..	..	..	..	..	0	0	..	0	0	0	25
..	17	..	..	..	..	..	..	..	..	0	0	..	..	..	..	25
1	14	..	..	..	..	..	..	..	0	0	0	..	0	..	..	26
..	..	..	..	..	..	..	..	..	..	..	0	0	..	..	..	25
1	104	8	..	..	..	..	..	..	0	0	0	0	0	0	0	243
..	..	..	..	..	0	0	..	..	..	..	..	..	..	..	..	25
..	..	..	..	0	0	0	..	..	..	..	..	..	..	..	..	25
..	..	..	..	0	0	0	..	..	..	..	..	..	..	..	..	25
..	..	..	..	0	2 Ch-Ck	0	..	..	..	..	..	..	..	..	..	25
..	..	..	..	0	0	0	..	..	..	..	..	..	..	..	..	25
..	..	..	..	1 Ch-Ck	1 Ck 2 Ch-Ck	0	..	..	..	..	..	..	..	..	..	25
..	..	..	..	0	0	0	..	..	..	..	..	..	..	..	..	25
..	..	..	..	0	0	0	..	..	..	..	..	..	..	..	..	25
..	..	..	..	0	0	..	..	..	..	..	..	..	..	..	..	25
..	..	..	..	0	2 Ch-Ck	0	..	..	..	..	..	..	..	..	..	25
..	..	..	..	0	0	1 Ck	..	..	..	..	..	..	..	..	..	25
..	..	..	..	1	7	1	..	..	..	..	..	..	..	..	..	275
..	..	..	0	..	..	..	..	..	..	..	..	..	..	..	..	25
..	..	..	0	..	..	..	..	..	..	..	..	..	..	..	..	26
..	..	..	0	..	..	..	..	..	..	..	..	..	..	..	..	25
..	..	..	0	..	..	..	..	..	..	..	..	..	..	..	..	25
..	..	..	0	..	..	..	..	..	..	..	..	..	..	..	..	34
..	..	..	4 Ck	..	..	..	..	..	..	..	..	..	..	..	..	25
..	..	..	0	..	..	..	..	..	..	..	..	..	..	..	..	3
..	..	..	0	..	..	..	..	..	..	..	..	..	..	..	..	11
..	..	..	2 Ck	..	..	..	..	..	..	..	..	..	..	..	..	25
..	..	..	0	..	..	..	..	..	..	..	..	..	..	..	..	25
..	..	..	0	..	..	..	..	..	..	..	..	..	..	..	..	25
..	..	..	6	..	..	..	..	..	..	..	..	..	..	..	..	249
2	..	..	..	..	..	..	..	3 Co-Ck	0	..	..	..	..	..	..	5
23	..	..	..	..	..	..	..	..	7 Co-Ck	..	..	..	..	..	..	30
10	..	..	..	..	..	..	..	..	4 Co-Ck	..	..	..	0	..	..	16
5	..	..	..	..	..	..	..	..	1 Co-Ck	..	..	..	..	..	..	6
7	..	..	..	..	..	..	..	..	3 Co-Ck	..	..	..	..	..	..	10
2	..	..	..	..	..	..	..	..	3 Co-Ck	..	..	..	..	..	..	5
2	..	..	..	..	..	..	..	..	2 Co-Ck	..	..	..	..	..	..	4
3	..	..	..	..	..	..	..	..	8 Co-Ck	..	..	..	..	..	..	11
5	..	..	..	..	..	..	..	..	1 Co-Ck	..	..	..	..	..	..	6
6	..	..	..	..	..	..	..	..	11 Co-Ck	..	..	..	..	..	..	17
24	..	..	..	..	..	..	..	..	6 Co-Ck	..	..	..	..	..	..	30
19	..	..	..	..	..	..	..	..	11 Co-Ck	..	..	..	..	..	..	30
21	..	..	..	..	..	..	..	..	7 Co-Ck	..	..	..	..	..	..	28
29	..	..	..	..	..	..	..	3	64	..	..	..	0	..	..	198
..	..	..	..	0	5 Ch-Ck	1 Ch 1 Ch-Ck	0	..	..	..	..	0	..	..	..	80
..	..	..	..	..	0	0	..	..	..	..	..	..	..	..	..	4
..	..	..	..	..	0	1 Ch-Ck	..	..	..	..	..	0	..	..	..	12
..	..	..	..	0	..	0	..	..	..	..	..	..	..	..	..	5
..	..	..	..	0	5	3	0	..	..	..	..	0	..	..	..	161

TABLE VIII. Results of processing through the key samples of salmon sampled in various commercial fishing areas along the British Columbian, Alaskan and Asian coast from 1956 to 1963. Table shows numbers and percentages of individuals classified into various species categories.

Species		Category									Total
		Sockeye	Pink	Chum	Coho	Chinook	Pink or Chum	Pink, Chum or Chinook	Chum or Chinook	Coho or Chinook	
Sockeye	No.	243	0	0	0	0	0	0	0	0	243
	%	100.0	0	0	0	0	0	0	0	0	100.0
Pink	No.	0	243	0	0	6	0	0	0	0	249
	%	0	97.6	0	0	2.4	0	0	0	0	100.0
Chum	No.	0	0	266	0	2	0	0	7	0	275
	%	0	0	96.7	0	0.7	0	0	2.6	0	100.0
Coho	No.	0	0	0	131	0	0	0	0	67	198
	%	0	0	0	66.2	0	0	0	0	33.8	100.0
Chinook	No.	0	0	1	0	93	0	0	7	0	101
	%	0	0	1.0	0	92.1	0	0	6.9	0	100.0

TABLE IX. Results of processing through the key (adjusted by omitting reference to more than one ocean annulus) samples of salmon sampled in various commercial fishing areas along the British Columbia coast in 1963. Table shows the numbers and percentages of individuals classified into various species categories.

Species		Category								Total
		Sockeye	Pink	Chum	Coho	Chinook	Chum, Pink or Chinook	Chum or Pink	Coho or Chinook	
Sockeye	No.	400	0	0	0	0	0	0	0	400
	%	100.0	0	0	0	0	0	0	0	100.0
Pink	No.	0	393	0	0	0	5	1	0	399
	%	0	98.5	0	0	0	1.3	0.2	0	100.0
Chum	No.	0	1	319	0	0	21	59	0	400
	%	0	0.3	79.7	0	0	5.3	14.7	0	100.0
Coho	No.	0	0	0	53	0	0	0	315	368
	%	0	0	0	14.4	0	0	0	85.6	100.0
Chinook	No.	0	0	0	3	136	3	0	258	400
	%	0	0	0	0.7	34.1	0.7	0	64.5	100.0

TABLE X. Results of processing through the key (adjusted by omitting reference to more than one ocean annulus) samples of salmon sampled in various commercial fishing areas along the British Columbian, Alaskan, and Asian coasts from 1956 to 1963. Table shows the numbers and percentages of individuals classified into various species categories.

Species		Category								Total
		Sockeye	Pink	Chum	Coho	Chinook	Chum, Pink or Chinook	Chum or Pink	Coho or Chinook	
Sockeye	No.	243	0	0	0	0	0	0	0	243
	%	100.0	0	0	0	0	0	0	0	100.0
Pink	No.	0	243	0	0	6	0	0	0	249
	%	0	97.6	0	0	2.4	0	0	0	100.0
Chum	No.	0	8	217	0	2	7	41	0	275
	%	0	2.9	78.9	0	0.7	2.6	14.9	0	100.0
Coho	No.	0	0	0	114	0	0	0	84	198
	%	0	0	0	57.6	0	0	0	42.4	100.0
Chinook	No.	0	0	0	0	86	9	0	6	101
	%	0	0	0	0	85.2	8.9	0	5.9	100.0

was mistakenly classified as being a chinook. Of the 101 chinook sampled, 93 (92.1%) were identified precisely and 7 (6.9%) fell into the mixed "chum or chinook" category. Only one was wrongly classified (as a chum). Almost one-third (67 or 33.8%) of the 198 cohos sampled had distinctive enough scales to permit precise identification of species — a higher fraction of "identifiable" individuals than among the standards (14.7% — see Table IV). All of the remaining 131 (66.2%) fell into the mixed "chinook or coho" category. None was incorrectly classified.

Thus, the key proved effective in identifying precisely the species of well over 90% of the sockeye, pinks, chums, and chinooks tested and one-third of the cohos. Where precise identification was impossible, in most cases the species was correctly designated as being one of two possibilities (e.g. chum or chinook *or* coho or chinook).

It should be noted that sections of the key are based on the number of marine annuli present. Separations achieved on the basis of this character result mainly from the fact that pink and coho salmon almost never spend more than one winter in the sea, whereas the other species typically spend more than one winter in the sea before maturing. This difference is useful for separating maturing fish but is of limited value for identifying samples of immature salmon taken on the high seas where pinks, chums, cohos, and chinooks occur together in their second year. An indication of the degree of separation that would be achieved among such samples of immature salmon can be gained by processing the samples, ignoring the sections of the key dealing with the number of marine annuli.

The results achieved by processing the standards and other samples in this way are summarized in Tables IX and X. Again 100% of the sockeye and almost 100% of the pinks keyed out precisely. However, the percentage of identifiable chums was lower; 79.7% compared to 94.7% for the standards and 78.9% compared to 96.7% for the other samples (Tables IV and VIII). The percentage of cohos that keyed out precisely was slightly lower. Percentages for chinooks were very much lower for the standard samples (34.1% using the second key compared to 93.2% for the first) but only slightly lower for the other samples (85.2%, compared to 92.1%). The reason for the difference in precision in classification of the two sets of chinooks was that the standard samples contained a relatively high proportion of individuals that had spent their first year in fresh water (similar to cohos). Most chinooks in the latter category subsequently spend more than 1 year in the sea and so exhibit more than one marine annulus on reaching maturity. The ability to separate such chinooks from cohos is greatly diminished if reference cannot be made to the number of marine annuli.

Thus for sockeye, pinks, and coho, the power of separation of the key for immatures was about the same as that for the matures but the ability of the key to identify precisely chums and chinooks was lower.

ACKNOWLEDGMENTS

The assistance of Mrs S. A. M. Ludwig, Mrs M. M. Aarts, and Mrs J. S. R. Rolfsen in processing the scales is gratefully acknowledged. The authors would also like to thank Mr F. C. Withler, Mr T. H. Butler, Dr R. E. Foerster, and Dr P. A. Larkin for their advice and helpful criticisms.

REFERENCES

CLEMENS, W. A., AND G. V. WILBY. 1961. Fishes of the Pacific Coast of Canada. *Bull. Fish. Res. Bd. Canada*, No. 68, 425 pp.

GILBERT, C. H. 1911. Age at maturity of the Pacific Coast salmon of the genus *Oncorhynchus*. *Report of the Commissioner of Fisheries of British Columbia*, pp. 57–70.

KOO, T. S. Y. 1962. Differential scale characters among species of Pacific salmon, pp. 127–135. *In* Studies of Alaska red salmon. University of Washington Press, Seattle.

MCMURRICH, J. 1912. The life cycles of the Pacific coast salmon belonging to the genus *Oncorhynchus* as revealed by their scale and otolith markings. *Trans. Roy. Soc. Canada*, No. 6, Sect. IV, pp. 9–28.

Dispersion of Kraft-Mill Effluent from a Submarine Diffuser in Stuart Channel, British Columbia[1]

By Michael Waldichuk

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Stuart Channel is a stratified, estuarine region typical of British Columbia coastal "inside" waters. Tidal currents are mostly less than 1 kt at all depths, and set to the northwest on the flood and southeast on the ebb, along the axis of the channel. Effluent released by a submarine diffuser, from the kraft pulp mill at Crofton, mixes in a ratio of about 1:22 with sea water as it rises to the surface. The entrainment of cold, saline water in the ascent gives the effluent–sea-water mixture at the "boil" above the diffuser a density usually greater than that of surface sea water. Therefore, the mixture generally sinks and spreads in a thin sheet at a depth between 3 and 10 m. Non-tidal currents at the surface and at 9–10 m depth could be expected to give the effluent present in these layers a net displacement seaward through Sansum Narrows. Effluent at a depth of 4–5 m would receive a net transport in the opposite direction (northwest) and could be expected to be retained in the channel much longer.

INTRODUCTION

In early 1958 a full-bleached kraft pulp mill of about 500 tons/day commenced operation in Crofton, British Columbia. A small industry of oyster production had been established in Stuart Channel (Fig. 1) not too far away from the pulp-mill site, some years previously (Quayle, MS, 1964). A problem arose in conflicting water uses as soon as it was announced by the pulpmill company that wastes would be discharged into Stuart Channel. Therefore, a considerable amount of study and planning had to go into the design of a suitable effluent discharge system so that the oyster populations would not be exposed to high concentrations of harmful substances in the mill wastes.

The first survey conducted in Stuart Channel in the vicinity of Crofton (Osborn Bay), during November 1954, showed that discharge of wastes directly into the harbour would be inadmissible if damage to the oysters were to be avoided (Waldichuk, MS, 1954; 1955). Moreover, the high concentration of pulpmill effluent that would be present in the surface waters from a near-shore surface discharge could conceivably harm the valuable spring and coho salmon runs through Stuart Channel into both Bonsall Creek and Chemainus River. This survey, and a subsequent one in 1955 (Waldichuk, 1958), showed that disposal of wastes into Stuart Channel by way of a submarine outfall could probably achieve rapid dilution and dispersion by turbulent mixing and tidal currents.

Surveys have been continued in Stuart Channel from year to year to determine the normal oceanographic characteristics and changes associated with

[1]Received for publication May 27, 1964.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

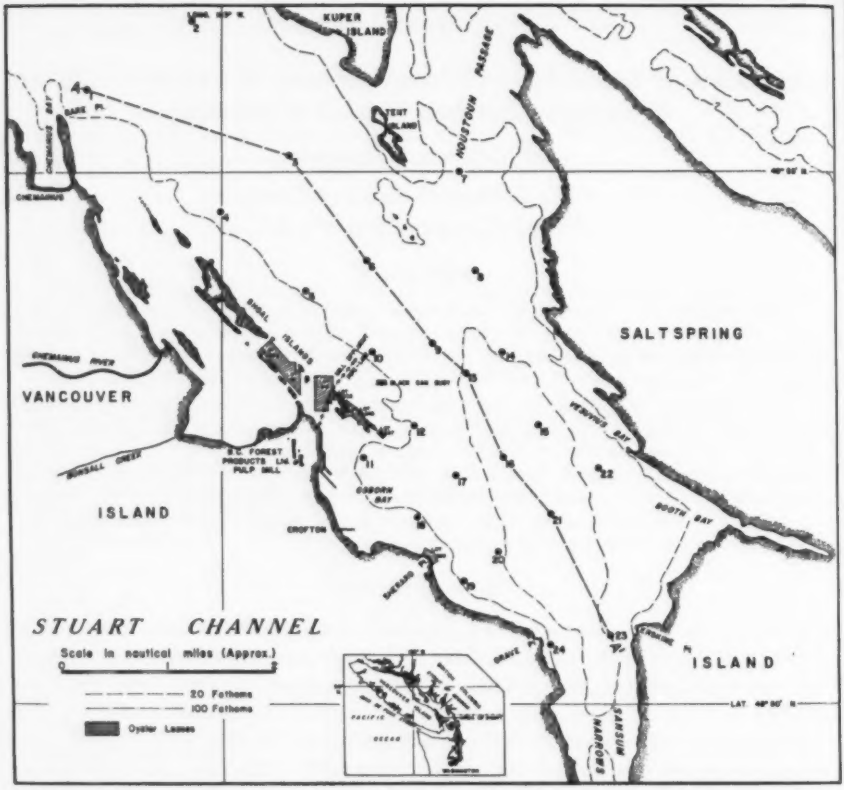


FIG. 1. Chart of Stuart Channel in the vicinity of the pulp mill at Crofton, showing the effluent pipe-line and adjacent oyster leases. Stations occupied during the survey of July 1959 are given in heavy circles.

pulpmill waste disposal (unpublished data). Condition factor determinations have been carried out on oysters in the Crofton area and compared with those of Ladysmith Harbour oysters for some time before and after the Crofton pulp mill went into operation (Quayle, MS, 1964). Some of the observations on the oceanographic characteristics and particularly on the dispersion and distribution of kraft pulpmill effluent in Stuart Channel from the submarine diffuser will be described in this paper.

THE SUBMARINE OUTFALL

During negotiations with the pulpmill company on the effluent disposal problem at Crofton, arranged by the Department of Fisheries, it was early agreed that the effluent would not be discharged into the harbour but that consideration would be given to installation of an outfall into Stuart Channel. It was further agreed that the effluent should be released at a suitable depth

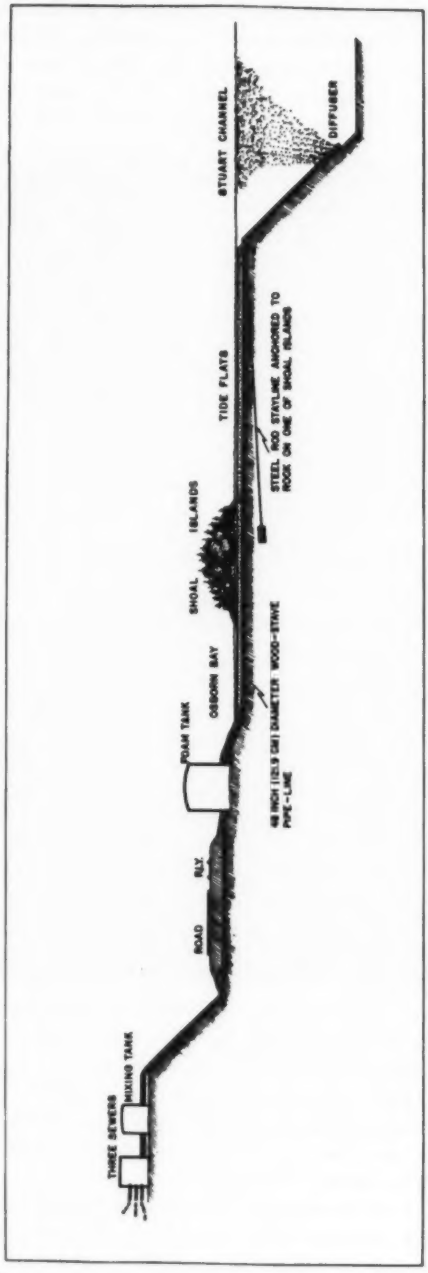


FIG. 2. Schematic diagram of the effluent pipe-line from the Crofton pulp mill into Stuart Channel.

and at a sufficient distance from the Shoal Islands so that high concentrations of harmful substances could be prevented from reaching the nearby oyster leases.

The preliminary proposals showed that the effluent from the pulp mill would consist of three separate streams: (1) acidic bleach-plant effluent, (2) alkaline extraction effluent, and (3) the kraft pulping wastes with general mill sewage and drainage. These would be combined in a mixing tank and then passed by pipe-line down a steep incline to a foam tank located on the shore. From there, the effluent would be conveyed by a pipe-line to the 10-fm contour on the outside of the Shoal Islands (Fig. 2). The initial rate of effluent discharge was to be about 32 million US gal/day (49.5 ft^3/sec or 1.40 m^3/sec). The piped effluent would contain all the plant wastes except that from the woodroom.

The pipe-line was constructed of treated wood staves held together by stainless steel bands. It was made up of sections 50 ft (15.3 m) long and 48 inches (122 cm) in inside diameter. The sections were linked by leak-proof couplings which gave some flexibility to the pipe-line even though it was held together quite securely. Full length of the line was about 5000 ft (1.5 km) from the foam tank to the end of the diffuser. The line was buried in a specially dredged channel across the tide-flats and finally terminated in deep water on the steep slope of the drop-off from the flats. The diffuser was located at an outward bulge in the 10-fm contour which allows the released effluent to be intercepted by the prevailing flow of currents in Stuart Channel. A gas-escape vent was inserted into the pipe-line, approximately one-half way between the foam tank and the outfall. This was designed to allow escape of excess gases that might form during the mixing of the effluent components in transit to the discharge point.

Difficulty was encountered during the first 2 months of operation of the pulp mill when the sections of the pipe-line near the diffuser parted. This was apparently due to movement caused by the oscillatory action of the tides, currents, and wind waves on a rather unstable bottom. On advice of a consultant specialist in deltaic structures, the end of the pipe-line was modified to make provision for a stay line to be fastened near the diffuser and anchored to the solid rock substratum of the nearest Shoal Island. The pipe-line and diffuser had to be modified to accommodate this change in anchoring, but the location of the end of the outfall remains approximately the same.

The altered diffuser consists of a 42-inch (107-cm) fiberglass-reinforced plastic pipe with a section 40 ft (12.2 m) long perforated with holes along its upper side. The holes are 6 inches (15.2 cm) in diameter, spaced 24 inches (61 cm) apart (centre to centre along the axis of the pipe), giving a total of 20 ports. They are located at about 25° from the vertical and are staggered so that successive ports alternate from one side of the pipe to the other. The last 7.5 ft (2.3 m) of the diffuser contains a deflector vane sloping upward at about 13° to the end. The vane reduces the end opening to one-half the diameter of the pipe and deflects the effluent upward.

Figure 3 is an aerial photograph of Stuart Channel showing the location of the effluent pipe-line and the end of the outfall, the streak of foam identifying the direction of movement of surface water with the ebb tide.

FIG. 3. Aerial photograph of Stuart Channel, taken September 17, 1962, on an ebbing tide, showing the location of the effluent pipe-line and the streaks of foam from the outfall. (B.C. Government Air Photograph.)

OCEANOGRAPHIC CHARACTERISTICS OF STUART CHANNEL

Typical of the channels among the Gulf Islands along the southeast coast of Vancouver Island, Stuart Channel is quite stratified in both salinity and temperature. Runoff from the Chemainus River and Bonsall Creek gives a certain amount of low-salinity water in the channel locally. Sea water enters the area through Sansum Narrows from the south, and through Houstoun Passage and other channels connecting with the Strait of Georgia to the east and north. Because of the tidal mixing which occurs in these channels during the transit of the water, the salinity in the deep water is somewhat lower than that present in the nearby waters of the Strait of Georgia and Haro Strait. The low salinity in winter at the surface is a result of local runoff and in the spring and summer it may be partly due to the Fraser River, which is in freshet at that time and sends its waters across the Strait of Georgia.

Tides in Stuart Channel are of the mixed type with two highs and two lows in one tidal day. There is a large diurnal inequality reflected in a large difference in the two successive low tides. Currents in Stuart Channel are largely tidal with some local effects from winds. Winds blow predominantly from the northwest in summer, from the southeast and southwest in winter.

Distribution of Properties

The vertical distribution of salinity in Stuart Channel shows a range from as low as 20‰ at the surface to almost 30‰ near the bottom. A vertical section through Stuart Channel is shown in Fig. 4 for the survey of July 1959.

The large changes in salinity with depth occur in the upper 50 m, the range being from 23.4‰ at the surface to 29‰ at 30 m in the July 1959 survey. Below the shallow halocline there were relatively small changes in salinity, an increase by less than 1‰ occurring between 30 m and the bottom, where it was approximately 29.8‰. Except for the surface layer, which is affected by seasonal runoff, there is little change in the vertical salinity distribution in Stuart Channel seasonally and from year to year.

Temperature distributions in Stuart Channel respond strongly to the seasonal heating cycle. As shown in Fig. 4 for July 1959, there were relatively high temperatures of 19–20°C in the surface layer. A large vertical gradient in temperature normally exists in the upper 15–20 m during this time of year. A 10°C range in the upper 30 m is contrasted with approximately a 1°C change in the next 150 m extending to the bottom. The large temperature stratification in the surface layer during the summer enhances the stability in terms of the density distribution. During the winter months, when heating is considerably less, and the surface temperatures may become even lower than those in the deep water, the stability of the water column is considerably reduced. At this time of year, there may be actually a positive vertical gradient in temperature in the surface layer, depending on the air temperatures.

The density, as represented by σ_t lines shown in Fig. 4, follows fairly closely the salinity and temperature distribution in summer. High temperature combines with low salinity to give the surface water a comparatively low density

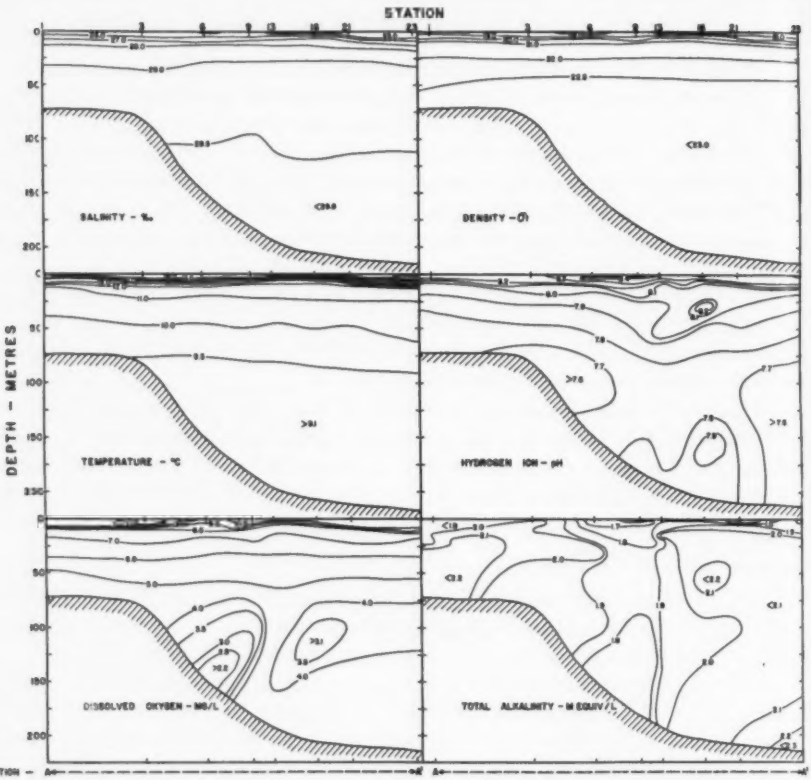


FIG. 4. Vertical distributions of properties in a longitudinal section A–A′ through Stuart Channel (see Fig. 1), observed July 8–11, 1959.

while the deep water remains fairly cold, saline, and quite dense. The density stratification at this time of year is very marked and the water column is extremely stable to mixing processes. The relatively calm conditions, which prevail during the summer season, do not seriously disturb the vertical pattern of density distribution. However, in winter when mixing can be much more vigorous and temperature is not effective in maintaining vertical density stratification in the water column, the waters are mixed more readily, which becomes evident following extreme storms. At this time of year, under the effects of strong winds and large tides, the waters in the deep part of Stuart Channel are replaced more rapidly than during the summer period.

Dissolved oxygen distribution is characterized by a relatively large vertical gradient in the upper layer, from high concentrations at the surface to moderately low concentrations at 50 m. Below this layer, the change with depth is comparatively slow but pockets of oxygen-deficient water may occur in certain areas, as shown near the bottom of the dissolved oxygen section in Fig. 4. This low

concentration could be associated with pulpmill effluent, but it is more likely a manifestation of the intrusion of oxygen-deficient waters from areas where oxygen depletion occurred by natural processes. The dissolved oxygen maxima near the surface are products of active photosynthetic processes by phytoplankton. Winter and early spring distributions of dissolved oxygen are somewhat more uniform vertically, and concentrations are higher at all depths than observed in summer. Concentrations at intermediate and near-bottom depths were at about 8 mg/l during a survey conducted in April 1959, compared to about 4 mg/l in July 1959.

The pH variability in a vertical section is not too different from that of the dissolved oxygen distribution. There is the typically large range of pH, from 8.4 to 7.9, in the upper 25-m layer. Maxima in layers near the surface correspond to the maxima in dissolved oxygen, where photosynthesis removes carbon dioxide from the water rendering it more alkaline. The deep water is characteristically lower than 7.9 in pH and is probably acidified slightly by the release of carbon dioxide in normal processes of decomposition of organic materials. The cell of low pH, nearly 7.6, at the slope of the bottom near the north end of the section (Fig. 4) was coincident with low dissolved oxygen.

Total alkalinity distributions follow to some extent the distributions of salinity with which they are closely related. However, in the survey of July 1959, there were rather strange deviations from a regular pattern of distribution in the deep water which are not clearly understood and which may not have too much significance. There may have been some effect of kraft-mill effluent shown in the relatively low alkalinity values in the middle of the Stuart Channel section (Fig. 4), but at the southern end (Stations 21 and 23), there was a fairly normal distribution of total alkalinity from surface to the bottom.

Currents

The currents in Osborn Bay and Stuart Channel have been discussed to some extent previously (Waldichuk, 1955, 1958). The general surface flow through Stuart Channel is southeastward during the period of ebbing tide and northwestward during the flood. Winds can considerably modify the surface pattern of currents, and during an ebb with southeast winds there may be a clockwise eddy circulating through Osborn Bay. The nearshore current in the bay may flow in a direction opposite to the general flow in Stuart Channel. The topographic effect along the shoreline may also influence the current patterns, giving flows across the tidal flats which are quite different from those in mid Channel. There is, for example, a strong onshore flow through the Shoal Islands during the period of flood when water must move onto the tidal flats in the Bonsall Creek estuary to fill up a fair-sized embayment.

During July 1957, current observations were made with a CBI (Chesapeake Bay Institute) drag at the surface and with an Ekman current meter at 15, 30, and 60 ft (4.6, 9.1, and 18.3 m) near the proposed pulpmill outfall. These observations are shown in a polar plot in Fig. 5, and in a linear plot in Fig. 6.

Surface currents ranged on the average from about 5 cm/sec to 30 cm/sec with the strongest flow occurring during ebb. Instead of a regular reversing

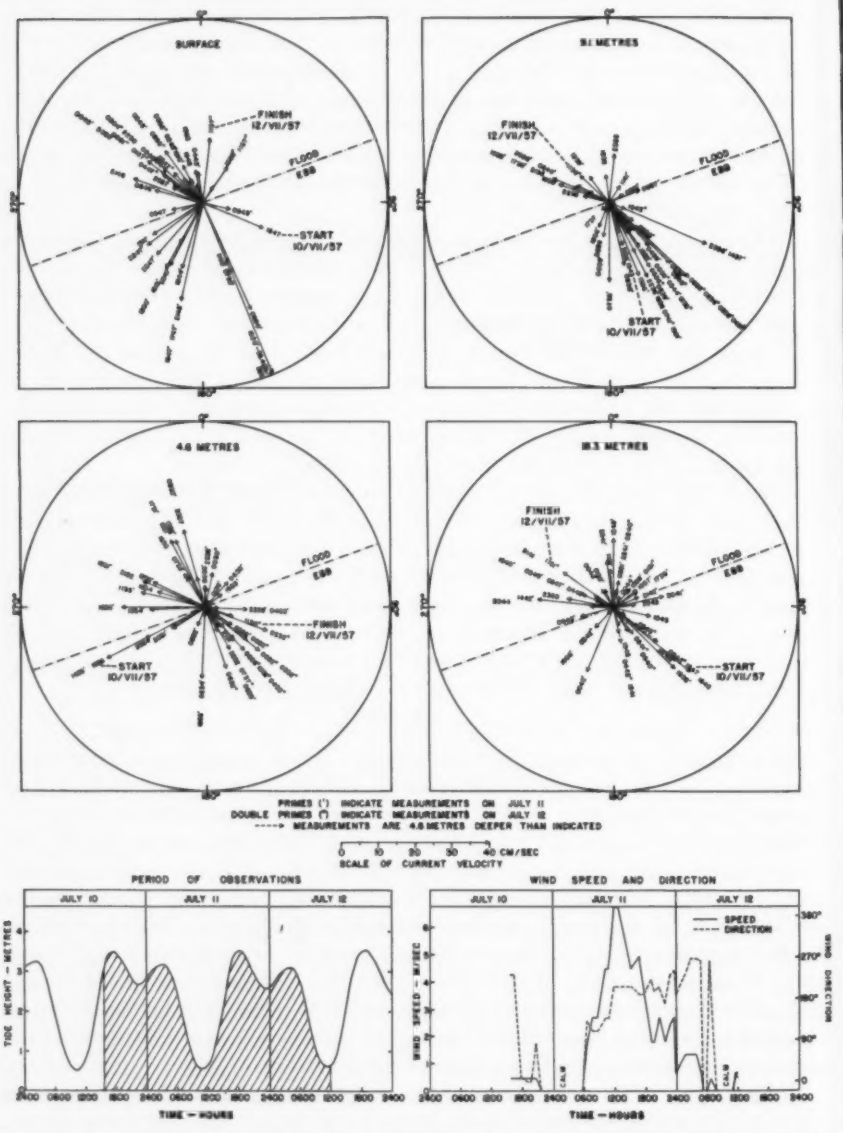


FIG. 5. Polar current diagrams for observations at various depths on Station 0-2, near the site of the pulpmill outfall diffuser in Stuart Channel, July 10–12, 1957. Lower diagrams give the tides and winds at time of current observations.

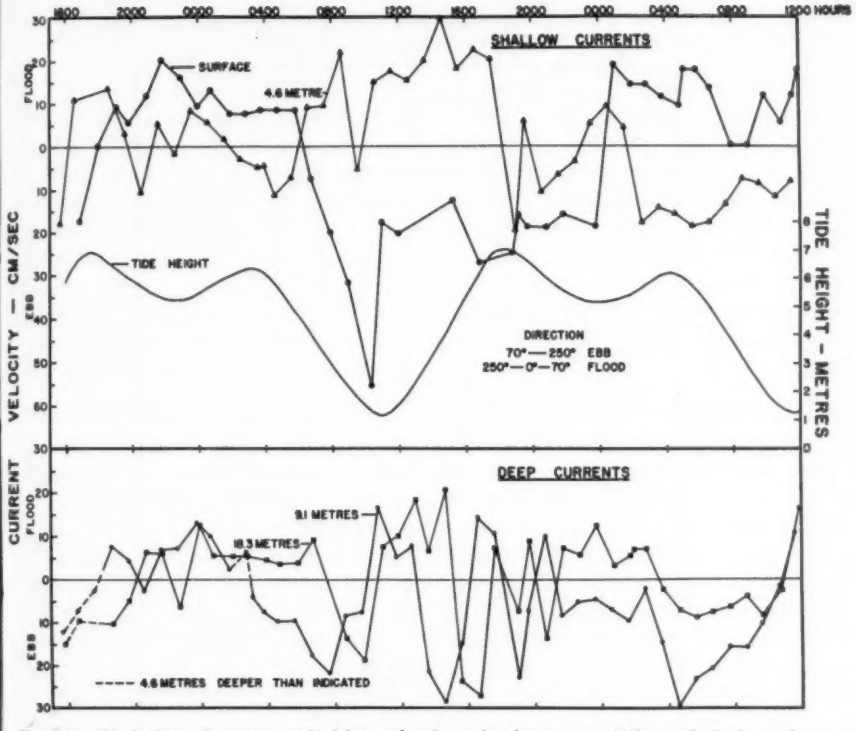


FIG. 6. Variation of current velocities at various depths over a 44-hr period of continuous observations at Station 0-2, July 10–12, 1957.

flow, the flood was directed generally along the axis of Stuart Channel toward the northwest, while the ebbing current set to the southwest. This may be due to the irregular configuration of the coastline south of the anchor station.

Currents at 4.6 m were generally at about the same strength as those at the surface but were directed more along a northwest–southeast line both on flood and ebb. The maximum currents were usually less than 25 cm/sec. Predominant flow at this depth appeared to be in the northwesterly direction. Currents at 9.1 m were weaker than those at 4.6 m and showed a greater tendency towards the southeasterly direction. Of all currents observed there appeared to be the least scatter in direction in the currents at 9.1 m. At 18.3 m, the currents were weakest of all those measured. The very small currents tended to be scattered in all directions, but there was a northwest–southeast trend for the stronger currents.

By integrating the current velocity vs. time curves shown in Fig. 6, using a planimeter to obtain the areas under the curves on flood and ebb for a full tidal cycle (24 hr, 50 min), the average tidal currents were obtained. Average flood velocities were .4.4, 8.2, 3.6, and 4.6 cm/sec at the surface, 4.6, 9.1, and

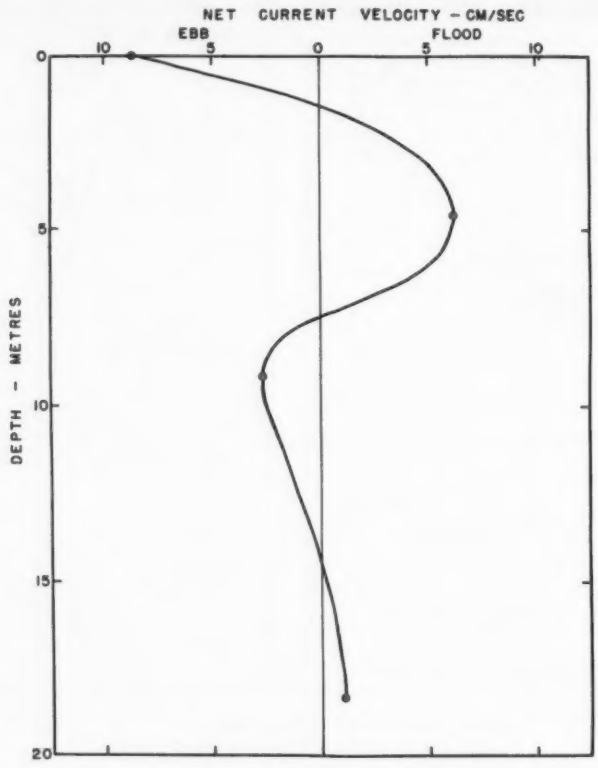


FIG. 7. Profile of net (non-tidal) currents at Station 0-2, determined for the period, 2000 hr, July 10, to 2100 hr, July 11, 1957.

18.3 m, respectively, while the corresponding ebb current velocities were 13.0, 2.0, 6.3, and 3.6 cm/sec. These values are somewhat higher than true average velocities, because the actual current data and not components in a given direction were plotted in Fig. 6. The net, non-tidal currents, obtained from the above averages for the various depths of current measurements, are shown in Fig. 7. This current profile is indicative of a three-layered system, where currents at the surface and 10 m exhibit a net flow to the southeast while the net current at 5 m sets in the opposite direction. There appears to be only a small residual current at 18.3 m, which in the observations of July 10–11, 1957, set to the northwest. It is doubtful whether there is a consistent residual current at depths below 15 m in the area of observations.

Current observations at the same anchor station have been conducted also during surveys in April and July 1959. These measurements confirmed in general the conclusions drawn from the earlier surveys.

VERTICAL DISTRIBUTION OF KRAFT-MILL EFFLUENT IN STUART CHANNEL

From the onset of pulpmill waste disposal through the pipe-line, there has been a distinct surface evidence of the discharge in the form of a surface "boil" having high concentrations of effluent above the diffuser. Surrounding the "boil", the surface sea water was usually relatively clear of effluent. Experiments with oysters held in trays at different points between the outfall and the Shoal Islands (Quayle, MS, 1964), were designed to provide exposure to oysters from regularly decreasing concentrations of effluent between the outfall and the island shores. Measurements of kraft-mill effluent (KME) in surface water samples above the oyster trays did not establish this to be the actual case. Instead, KME concentrations were sometimes higher in surface waters near the islands than they were near the outfall.

Experimental Evidence of Effluent Distribution Near the Outfall

From the foregoing observations, it was suspected that sinking of the effluent–seawater mixture was occurring around the perimeter of the "boil". Tests with rhodamine B dye injected into the "boil", as well as into the mixing tank on the shore, confirmed that sinking indeed does occur. The dye rapidly disappeared below the surface as it left the centre of the "boil". It could be detected by pumping water from different depths using a submersible pump (Sumo Pumps Inc., Stamford, Conn.) and by passing the water through a fluorometer (G. K. Turner Associates, Palo Alto, Calif., Model 111, with continuous flow door), used for continuous monitoring. The vertical profiles of dye concentration corresponded to KME concentrations in samples taken near the outfall and were confirmed later by *in-situ* measurements of transparency. The maximum concentrations of dye could be detected at depths between 3 and 8 m. Typical vertical distributions of dye near the outfall from releases into the "boil" (July 1961) and from injections into the pipe-line at the mixing tank (July 1963) are shown in Fig. 8. The units of dye concentration are arbitrary, given only for comparison of values at different depths in individual profiles.

Kraft-mill effluent concentrations were measured by a modified Pearl-Benson procedure (Barnes *et al.*, 1963). Kraft "black liquor" of about 16% total solids was used as a standard. The reagents were made up and added in the same manner as specified in the original procedure, and the absorbance of the treated samples was measured with a Beckman DU spectrophotometer, using cells of 10 cm light path at a wavelength of 410 mμ. Because of interference from certain natural substances which respond in the same way as KME and SSL (spent sulphite liquor) to the chemical treatment used in the Pearl-Benson method, apparent KME concentrations of less than 5 ppm (parts per million) are not considered significant. An effort has been made to base all KME results on the same standard, so that values should be consistent from one survey to another.

As shown in the left-hand panel of Fig. 8, there appeared to be two maxima, a minor one at the surface and a major one at 7 m, in the KME data for the

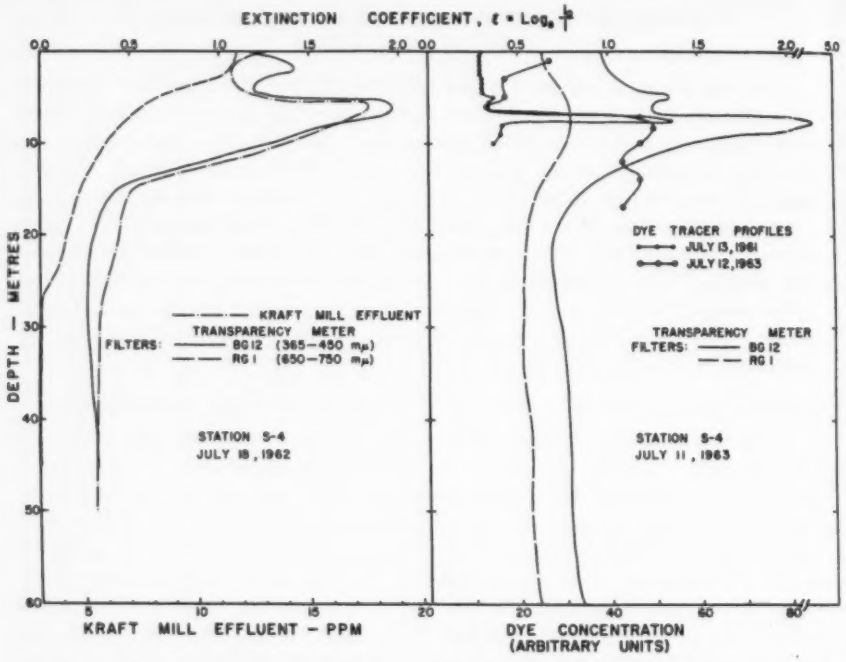


FIG. 8. Profiles of extinction coefficients, kraft-mill effluent and rhodamine B concentrations, at a station near the pulpmill outfall in Stuart Channel, during July in 1961, 1962, and 1963.

station occupied near the pulpmill outfall on July 18, 1962. There was a rapid decline in concentration to a depth of 15 m, below which little more than background levels of KME prevailed. Because sampling bottles were spaced at 4- and 5-m intervals below 6 m depth, other peaks in KME concentration could have been missed.

To corroborate the vertical distribution of wastes from the pulp mill, observed in KME determinations and dye tracer experiments, transparency measurements were conducted in surveys of July 1962 and July 1963. Measurements were made on an Askania Transparency Meter (Askania-Werke AG, Berlin-Friedenau, Germany) with 2 Jena glass filters giving light transmission maxima in the blue-green (No. BG 12 at 365–450 mμ) for one filter, and in the red-green (No. RG 1 at 650–750 mμ) portions of the visible spectrum for the other. In Fig. 8 are shown profiles of the extinction coefficient, ξ, computed for data obtained using the two filters. The extinction coefficient is defined by $\xi = \log_e \frac{I_o}{I}$, where I_o is the incident light intensity, I is the intensity of light transmitted by a thickness of 1 m of water *in situ*, and e(= 2.7183) is the base for natural logarithms. The extinction coefficients obtained with the BG 12

filter follow quite closely the KME concentration, particularly for the major peak observed at 6 m in July 1962. However, the RG 1 filter is apparently much less specific for the coloured dissolved constituents in kraft wastes and is more indicative of actual turbidity of the water. Transparency measurements were made at more closely-spaced intervals of depth at Station S-4 on July 11, 1963. A very large peak in the extinction coefficient was given by the BG 12 filter at 8 m, as shown in the right-hand panel of Fig. 8. This shows that the layer of effluent may be very thin and can be missed easily in the normal oceanographic procedure of widely-spaced sampling bottles.

Dispersion of Effluent Through Stuart Channel

Layers of relatively high concentration of effluent may be found one above the other, as shown in the sections of KME distribution in Fig. 9. Concentrations higher than 10 ppm are hatched to conveniently illustrate zones of moderately high concentration. These sections represent surveys taken as synoptically as possible with one ship, all stations being occupied in about 2 days. Different periods of the year during different years are represented so that the distributions may vary according to the changes in oceanographic characteristics, particularly in the surface layer. Moreover, the distributions may be related to the particular wind and tide conditions prevailing at the time of the survey.

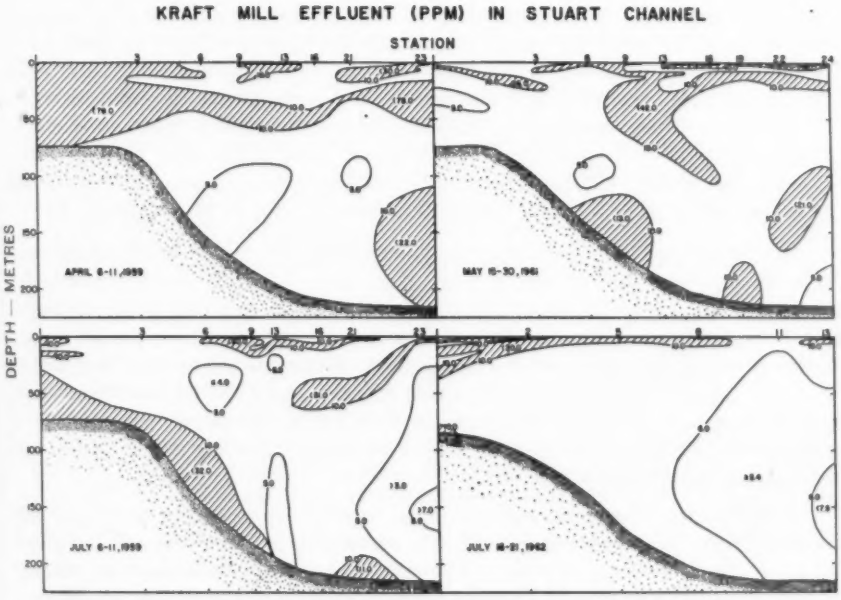


Fig. 9. Kraft-mill effluent concentrations in vertical distributions through Stuart Channel, approximately along section A–A′ shown in Fig. 1, as observed during different periods.

It appears that a subsurface layer of effluent forms and this is carried first southeastward with the ebb or northwestward with the flood, depending on the stage of the tide. Then, on the next tide, as the effluent layer is carried further afield, it becomes more diffuse and may be somewhat deeper than originally. Although the data do not represent truly synoptic pictures, the general pattern of a near-surface layer with a comparatively high KME concentration seemed to be repeated for all surveys.

The apparently high concentrations of KME observed in the northern part of the section on certain surveys may be related to something quite different than the pulpmill effluent. The Georgia Generating Station (thermal-electric plant), located on Bare Point near Chemainus, discharges wash waters containing certain organic and inorganic impurities extracted from fuel oil used in the power plant. These wastes may contribute a certain amount of organic material which responds to the test used for the KME determination. Another kraft pulp mill is located 20 nautical miles (37 km) to the northwest, near Nanaimo (at Harmac), but dilution of the effluent should be great enough to render it undetectable by the present method after it leaves Dodd Narrows (Waldichuk, MS, 1964).

As previously shown, from the current observations, there is a net flow southward at the surface and northwestward at 4–5 m depth in Stuart Channel. This means that the effluent from the outfall will be continuously displaced into Sansum Narrows if it is maintained at the surface, assuming that it is not carried out of Stuart Channel on the flood tide. Surface-borne effluent is flushed out of the system by tidal action and enters the channels leading to Haro and Juan de Fuca Straits. However, effluent which may contaminate the deep water as it leaves the diffuser could conceivably accumulate near the bottom until conditions were right for replacing the deep water. The deep-water concentration of kraft-mill effluent which appeared to be relatively high in some surveys could have resulted from near-bottom contamination occurring at the outfall.

The more common dispersion of effluent from the outfall region is by way of a subsurface layer between 3 and 10 m deep. During periods when the density of the surface water in Stuart Channel is such as to allow the effluent–seawater mixture from the "boil" to sink to a depth around 5 m, a net transport of the effluent to the northwest can be expected. Since seaward flushing is retarded by the topographical configuration in this direction, an accumulation of effluent can be expected to occur under these circumstances. However, effluent which sinks to a depth of 9–10 m may experience more rapid flushing action with a net transport toward Sansum Narrows.

Differences in the distribution patterns of KME from survey to survey are no doubt due to changes in the depth which the effluent–seawater mixture assumes after it leaves the "boil". The survey of July 1962 showed the effluent to be confined to a surface layer and flushing action was probably rapid, judging by the general lack of higher concentrations of KME in deeper water (see lower right-hand block of Fig. 9).

TURBULENT MIXING AND DILUTION OF KRAFT-MILL EFFLUENT AT THE OUTFALL

The turbulence caused by effluent discharging from the diffuser ports disturbs the structure of the water column above the outfall. To determine the effect of the rising effluent on the water structure, samples should be taken below the "boil" by means of a rapid-sampling device and temperature profiles by bathythermograph. It was difficult to obtain samples by standard sampling procedures while the survey vessel attempted to hold position in the "boil", because of a natural tendency to be shifted outward by the diverging action of the effluent–seawater mixture as it reaches the surface. However, a series of rapid bathythermograph casts were made and slides of temperature variation with depth were obtained. A typical BT record of temperature, shown in Fig. 10, illustrates the effect of turbulent mixing. The time and space variation of temperature in this highly dynamic region is reflected in the large difference between the upward and downward traces on the BT slide taken in the "boil". A more stabilized temperature profile was obtained in the less disturbed water on the edge of the upwelling region. The erratic fluctuations of temperature with depth in the former case indicate the effect of turbulence on the temperature structure of the water.

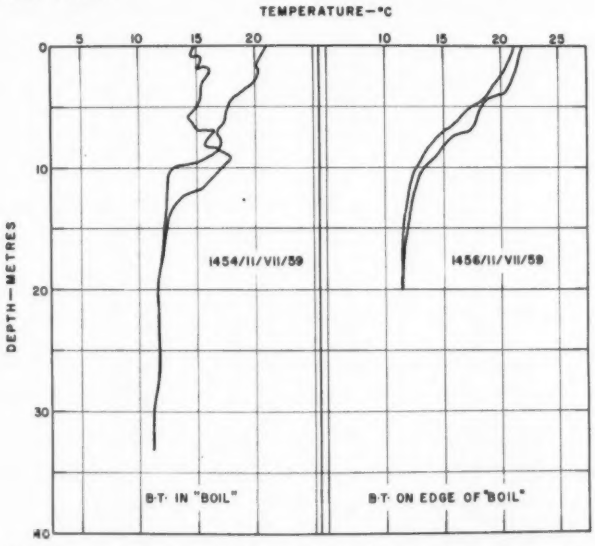


FIG. 10. Temperature profiles, obtained with a bathythermograph in the outfall "boil" and on the periphery, on July 11, 1959.

INITIAL DILUTION OF EFFLUENT DURING ITS ASCENT FROM THE DIFFUSER TO THE SEA SURFACE

By measuring the concentration of kraft-mill effluent in a series of surface samples obtained in the "boil", it is possible to obtain some statistical mean of KME in the effluent–seawater mixture as it reaches the surface. Samples were

taken at the outfall during periodic sampling of surface water at various locations in association with oyster-condition experiments conducted during the period 1958–1961 (Quayle, MS, 1964). KME data for these samples, as well as for those taken at the black can buoy, 600 yd (550 m) southeast of the outfall, are given in Table I. The concentrated total effluent was sampled on a number of occasions from the trunk sewer between the mixing tank and the foam tank on shore. KME concentrations in these samples are also given in Table I. From the KME concentration in the effluent–seawater mixture of the "boil" and that in the total effluent of the pipe-line, a range of dilution from 1:19 to 1:71 (ratio of effluent to seawater) was obtained. Because sampling at the outfall in the one case of high dilution could have missed the patches of high concentration

TABLE I. Kraft-mill effluent (KME) concentration in the effluent pipe-line from the Crofton pulp mill, and in the surface samples at the outfall (in the "boil"), and at the black can buoy in Stuart Channel.

Date (Day/Mo/Yr)	Tide[a] (at time of sampling at black can buoy)	KME concentration			Dilution above the diffuser (effluent:seawater)
		In the pipe-line	In the "boil"	At the black can buoy	
		ppm	*ppm*	*ppm*	
27 Nov. 58	Small flood	2220	29.5	7.2[b]	1:70.9
7 Aug. 59	HLW	1400	66.2	5.7	1:20.1
8 Aug. 59	Small flood	1410	62.8	8.1[b]	1:21.5
20–21 Jan. 59[c]	HLW	...	35.7	5.1[b]	...
16 Feb. 59	Large ebb	...	45.9	4.9[c]	...
11 Apr. 59	Large flood	...	57.2	7.1	...
12 May 59	LLW Start of large flood	...	90.8	6.7	...
8 June 59	Large flood	...	63.8	4.8	...
10–11 July 59[f]	LHW	...	121.8	10.9	...
18 Aug. 59	Large flood	...	120.2	4.0	...
30 Oct. 59	Small flood	...	79.7	8.6[d]	...
10 Dec. 59	HHW	...	79.0	10.0	...
18 Feb. 60	LLW	4770	239.0	16.5	1:19.0
9 Mar. 60	Small ebb	2875	108.1	14.4	1:25.6
15 Apr. 60	Large ebb	...	139.0	23.0	...
12 May 60	Large flood	...	160.5	28.9	...
14 June 60	LLW	...	135.2	16.8	...
20 July 60	Large flood	...	32.5	12.4	...
19 Aug. 60	Large flood	...	121.3	13.0	...
22 Oct. 60	Small flood	...	137.9	24.0	...
17 Dec. 60	Small ebb	...	121.8	10.2	...
6 Jan. 61	HLW	...	47.2	15.4	...
16 Feb. 61	Small flood	...	89.5	9.5	...
20 Feb. 61	LLW	...	100.3	21.7	...

[a]HHW = Higher High Water; LHW = Lower High Water; LLW = Lower Low Water; HLW = Higher Low Water.

[b]Sample taken on oyster lease (Lot 345) on Shoal Islands.

[c]Sample location described as "between navigational light (on south end of Shoal Island) and outfall".

[d]Sample taken midway between black can buoy and Lot 345.

[e]Sample in "boil" taken on 20 Jan. 59 and at black can buoy on 21 Jan. 59.

[f]Sample at black can buoy taken on 10 July 59 and in "boil" on 11 July 59.

of effluent, that dilution value is probably not typical. Excluding the high value, dilutions from the other three samplings gave an average of 1:22.

Large differences, of course, occur from time to time in the KME in the total effluent released from the mill for various reasons related to plant operation. This is reflected in the KME data for the raw effluent sampled at different times as shown in Table I. With consistent mixing from the diffuser to the sea surface, the more concentrated raw mill effluent would lead to higher KME concentrations at the surface above the diffuser. Except for the one case of apparently high dilution, this appears to be generally true. However, oceano-

TABLE II. Variation of properties at the surface in the "boil", above the pulpmill diffuser in Stuart Channel, 1958–1959.

Sample* No.	Time (PST) and date	Tide	Depth of water above diffuser	Salinity (‰)	Temp. (°C)	Density (σ_t)	KME (*ppm*)
			m (approx.)				
1	1318/8 Aug. 58	LHW	20.7	27.14	...	...	66.2
2	1602/11 Apr. 59	Rising (Large flood)	18.8	27.36	9.8	21.06	57.2
3	1436/11 July 59	LLW	18.7	25.24	22.0	16.87	9.9
4	1438/11 July 59	Rising	18.7	25.19	21.3	17.01	7.2
5	1449/11 July 59	"	18.8	25.39	18.9	17.76	46.1
6	1454/11 July 59	"	18.8	25.63	16.4	18.51	121.8
7	1504/11 July 59	"	18.9	25.14	14.9	18.45	7.2
8	1509/11 July 59	" (Large flood)	19.0	25.89	20.2	17.82	154.2
9	1515/11 July 59	"	19.0	25.12	20.4	17.18	6.1
10	1732/11 July 59	"	20.0	26.14	13.8	19.43	130.1
11	1956/11 July 59	"	21.7	26.16	14.2	19.37	95.3
12	2044/11 July 59	HHW	22.2	26.08	13.8	19.39	81.0
13	2335/11 July 59	Falling (Small ebb)	21.4	25.89	14.5	19.10	62.0
14	0206/12 July 59	"	19.9	24.91	16.5	17.94	37.0
15	0445/12 July 59	HLW	19.4	25.10	17.4	17.89	104.3
16	0711/12 July 59	Rising (Small flood)	20.4	26.20	13.6	19.51	94.8
17	0930/12 July 59	LHW	21.3	26.25	13.6	19.55	108.7
18	1043/12 July 59	Falling (Small ebb)	21.0	25.91	14.0	19.21	78.2
19	1307/12 July 59	"	19.9	25.68	14.6	18.92	96.8

*Samples No. 1–9 were collected during synoptic oceanographic surveys, No. 3–9 being taken on a S–N traverse over the outfall, within a 150-m radius of the "boil". Remaining samples were taken in the "boil" during the course of current observations at an anchor station.

graphic characteristics should provide better conditions for initial dilution of the effluent in winter than in summer, owing to the less stratified density distribution and greater exposure to wind mixing at the surface.

Because of patchiness in KME concentrations in the "boil", large variations may occur from sample to sample taken in a short space of time. Changes in water depth above the diffuser with the changing tide may also introduce variations in the amount of dilution effected during the ascent of the effluent to the surface. A series of samples taken approximately every 2 hr at the outfall "boil", during a 20-hr period in July 1959, was analyzed for KME concentration as well as for salinity. Temperatures were also recorded, which allowed the density (σ_t) to be evaluated by the standard method for sea water. Variations of these properties from sample to sample with the changing tide are shown in Table II.

Vertical Distribution of Effluent in Relation to Density Structure

From the data collected thus far, it is evident that the depth to which the effluent–seawater mixture descends after it leaves the "boil" is not constant even during the same season. A change in density characteristics of Stuart Channel can drastically alter the depth of spread of effluent away from the outfall. During two periods, about a month apart in the summer of 1959, observations were made on the vertical distribution of salinity, temperature, dissolved oxygen,

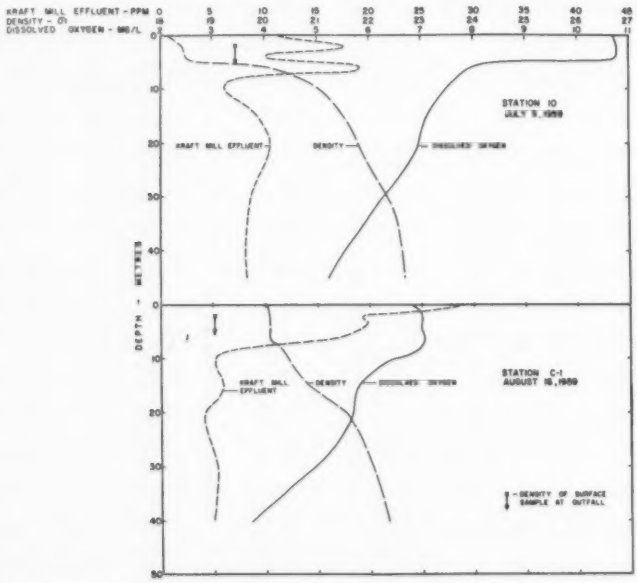


FIG. 11. Profiles of density, kraft-mill effluent, and dissolved oxygen concentrations at stations near the outfall in Stuart Channel during the summer of 1959.

and kraft-mill effluent concentration at a station near the outfall. At approximately the same time, samples of effluent–seawater mixture were taken at the surface of the outfall. Results are plotted in Fig. 11.

In the July 9 data, the stratified conditions in Stuart Channel are clearly shown with a low density in the surface water and a shallow pycnocline. The density of the effluent–seawater mixture taken from the "boil", at approximately $\sigma_t = 19.5$, was greater than that of the surface sea water, $\sigma_t = 18.2$, and was the same as that of the sea water surrounding the outfall at about 6 m depth. The major maximum in the KME concentration was found at the same depth. At this time there was a very large gradient in dissolved oxygen between the upper 4-m layer and the depth of 6 m. It is considered possible that the presence of KME in this near-surface layer was responsible for the rapid diminution with depth in dissolved oxygen concentration in the upper layer.

During the August 16 observations, the density profile in Stuart Channel had markedly changed from the July picture. Although the density of the effluent–seawater mixture was even less at this time ($\sigma_t = 19.1$) than it had been during the July survey, it did not exceed that of the surface sea water ($\sigma_t = 20.0$). Hence the mixture did not sink but apparently spread out on the surface of the channel. The profile of KME concentration clearly shows this pattern of distribution. There was a much-reduced dissolved oxygen concentration in the surface layer at this time from that observed in July. Part of this change may have been due to the normal decline in surface dissolved oxygen as the season progressed; but it is probable that the decomposition of the effluent in the surface water was also responsible for part of the oxygen reduction.

QUALITATIVE OBSERVATIONS ON EFFLUENT DISPERSAL FROM THE SUBMARINE DIFFUSER

Consisting mainly of fresh water and small quantities of dissolved organic and inorganic substances plus particulate material of wood origin and being usually fairly warm, kraft-mill effluent has a specific gravity slightly less than 1.0. This property gives it considerable buoyancy when it is placed into fairly cold, saline water with a density around 1.023 g/ml. Therefore, it would tend to rise if merely introduced into sea water at a depth of 20 m in Stuart Channel. The effluent possesses also a considerable amount of kinetic energy, derived from its large volume and gravitational flow from the mixing tank, approximately 72 ft (22 m) above mean sea level. Part of this energy is probably dissipated in friction along the pipe-line.

Effluent leaving the diffuser ports immediately comes into contact with sea water which surrounds the diffuser. Mixing with the sea water takes place through the turbulence which is created by the emerging jets of effluent. The upward momentum of the effluent carries it and the mixed-in sea water toward the sea surface entraining by aspirator action en route more sea water surrounding the rising column. Mixing of effluent and sea water along the perimeter of the rising column provides greater dilution than available at the

core. Consequently, uneven mixing occurs through the diameter of each column. Turbulence created in this rising effluent–seawater mixture utilizes some of the original kinetic and buoyant energy possessed by the effluent. Destruction of stratification in the sea water dissipates a large proportion of the turbulence energy.

When the mixture of effluent and sea water reaches the sea surface, it still has a considerable amount of upward momentum and appears as a slick region of upwelling in the form of a "boil". It contains only a small proportion of effluent on the average, mixed with a large amount of sea water. The concentration of effluent, of course, is not uniform throughout the whole surface of the "boil", because of non-homogeneous mixing in the jets emerging from individual ports and the presence of less contaminated sea water between the rising columns of mixture. During periods of calm sea and warm weather, the effluent–seawater mixture can be seen to plunge under the surface sea water around the edge of the "boil", usually marked by an accumulation of foam and detritus in a convergence line. Beyond this line the effluent is not apparent in high concentration at the surface. The diluted effluent spreads below the surface at a depth where it can mingle with sea water of density equal to its own. Under choppy conditions when surface mixing is fairly intense, effluent appears at the surface in a more widespread distribution. When surface sea water is higher in density than the effluent–seawater mixture, there is a surface spread of the effluent. A schematic diagram of the discharge of effluent from the diffuser, entrainment of sea water in its ascent to the surface, and spread of the effluent–seawater mixture from the "boil" is shown in Fig. 12.

From dye experiments, the movement from the "boil" could be observed to occur as a billowing drift of clouds of effluent in the direction of the prevailing

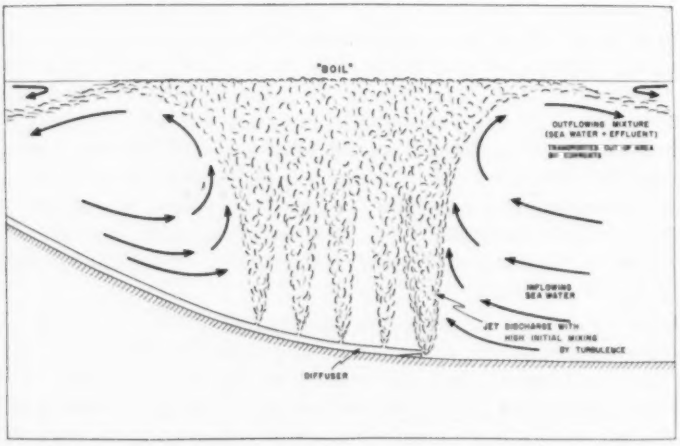


FIG. 12. Schematic representation of the process of initial dilution, rise, and spread of the pulpmill effluent emerging from the diffuser in Stuart Channel.

current. These clouds present cores of high effluent concentration surrounded by clearer sea water. This type of effluent distribution in the plume from the "boil" was noted in pulses of high dye concentration while monitoring at a given depth from an anchored vessel downstream from the outfall (Fig. 13). Some of the longer-period (20 min approximately) fluctuations in dye concentrations, shown in Fig. 13, may have been caused by internal waves in the pycnocline where the highest dye concentrations were found.

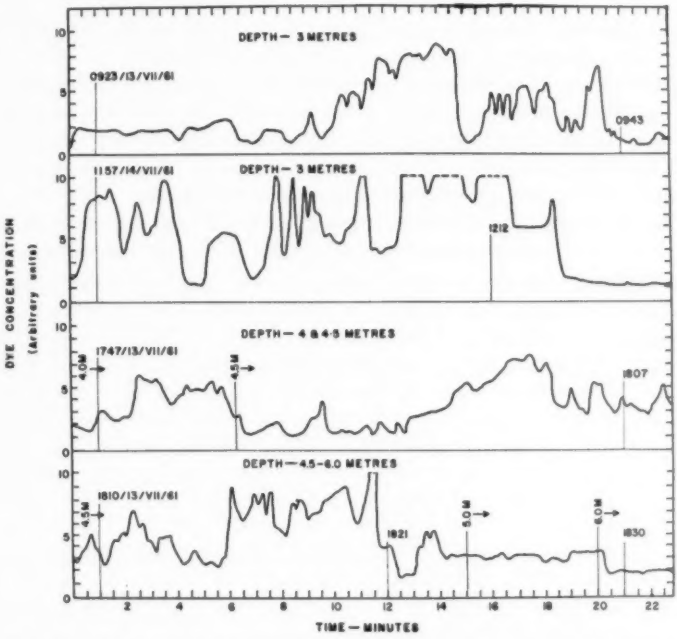


FIG. 13. Fluctuations in concentration of rhodamine B at given depths on fixed stations in Stuart Channel, just south of the pulpmill outfall, in July 1961.

An important aspect of marine dispersion of effluent is advection at the outfall. If currents were not present to remove effluent as it emerges from the diffuser and becomes mixed with sea water, intolerable local pollution would occur. Eventually the sea water in the area would become largely displaced and old effluent would be mixed with the new effluent as the wastes bubble to the surface from the diffuser. Fortunately, tidal currents in Stuart Channel transport the effluent fairly rapidly from the outfall. As the effluent leaves the "boil" in a thin layer at either some subsurface level or on the surface, depending on the density of the surface sea water, it first forms a plume, almost as a smoke plume leaving a stack, and then gradually forms a widening ribbon of effluent. This behaviour can be seen in aerial photos of Stuart Channel (Fig. 3). With

the changing tide, the ribbon of dilute effluent is twisted back into the channel, and depending on the currents at the depth of the effluent, it may diffuse throughout the width of the channel on subsequent tides or form only a meandering stream with cells of high concentration of effluent separated by areas of relatively unpolluted sea water.

DISCUSSION

One of the objectives in a study such as this is the establishment of a basis for future installations of submarine outfalls. It is common practice in design of a disposal pipe-line, given the requirements on dilution to meet the standards of maximum permissible concentrations of harmful substances, to essentially take a "shot in the dark" in locating the outfall at a "safe" depth and far enough from areas where contamination is to be avoided. In this approach it is only known that the pipe-line will carry the wastes from the shore to some point out at sea, where it can be anticipated from past experience that they will be diluted sufficiently and dispersed by turbulent mixing and currents.

What is needed in outfall design work is some knowledge on the behaviour of the effluent as it enters stratified waters, such as: (1) rate at which it emerges from the diffuser; (2) the height to which it will rise in the receiving waters; (3) whether it will sink if it reaches the surface and, if so, how deeply; and (4) the effect that stratification of the water will have on the ascent and mixing of the effluent. In some cases, it is advantageous to have all the effluent rise to the surface to be carried away by the strong surface current. In other cases, where aesthetic considerations are important, it is desirable that the industrial effluent or domestic sewage should not appear on the surface but should be dispersed in a submerged field. Some of the studies conducted experimentally and theoretically in the past on submarine waste disposal are reviewed in the following paragraphs.

A submarine, waste-disposal pipe-line to alleviate estuarine pollution (Eldridge and Orlob, 1951) was installed at Everett, Washington, in 1951, to serve the local pulp mills. The pipe-line extended to a depth of 300 ft (92 m) and discharged 22 million gal/day (0.966 m^3/sec) of effluent through a series of outlets in a 1000-ft (304-m) diffuser. The effect of this submarine disposal on waters in Port Gardner Bay was subsequently investigated (Orlob *et al.*, 1951; Callaway, MS, 1963). Diffusion of the effluent seaward in deep water was shown to occur with an oxygen minimum at 100 ft (30 m) depth resulting from the stabilization of spent sulphite liquor.

Shaw (MS, 1956), after studying the available means of effluent disposal from the Windscale reactor in northwestern England into the Irish Sea, came to the conclusion that: (1) a suitable depth of water should be chosen; (2) effluent density should be kept as different from that of sea water as possible; and (3) maximum use of wind as a mixing agent should be made, by selecting an exposed outfall site with the prevailing wind directed offshore. He further recommended (Shaw, MS, 1957) that the outfall be designed with many horizontal branches suitably spaced so that little or no mutual interaction would occur between different plumes of effluent.

In his study of conditions arising from the Hyperion sewage disposal into Santa Monica Bay, Gunnerson (1958) concluded that after initial dilution of the sewage, as measured from chlorinities, additional dilution is derived from turbulent mixing, which is effective for some 4 hr after discharge, and from lateral diffusion thereafter. The same investigator carried out dye-tracer experiments in Santa Monica Bay to determine rates of horizontal diffusion for application to the Hyperion outfall (Gunnerson, 1959). He showed that the data fit the 4/3-power law for diffusion quite well, with a difference of proportionality constant between the region where there are no boundary restraints and one confined by a shore-line on one side.

Brooks (1960) discussed, from a theoretical approach, a rational method of analysis for the turbulent diffusion of a sewage field in an ocean current. Lateral mixing in a sewage field was considered, and the exact solution was derived for the partial differential equation balancing diffusion, advection, and mortality of coliform bacteria. An expression was also obtained for the rate of spread of a sewage field assuming that diffusivity is proportional to the 4/3-power law of the length, given by an appropriate dimension in the sewage field.

A comprehensive review of theoretical models for turbulent diffusion in the sea, which might have some application to sewage and industrial waste disposal, has been published recently by Okubo (1962). Some of the theoretical predictions deduced from proposed distributions were critically compared with observed data by that author.

Rawn and Palmer (1930) carried out some of the earliest model studies and field investigations on the area and extent of a sewage field in sea water, when the quantity of sewage and direction and depth of discharge below the ocean surface are known. Their experiments provided strictly empirical relationships which bear closely on the conditions prevailing only in the coastal area of investigations, south of the City of Los Angeles. However, certain parameters were established which allowed later engineering studies to have a much sounder basis for outfall design than possible under previous circumstances. Pearson (1956) reviewed the problems of submarine outfall disposal and summarized the available knowledge until that time. Rawn *et al.* (1960) made a comprehensive study of diffusers for the disposal of sewage in sea water, based on investigations at the Whites Point outfall, adjoining Santa Monica Bay, Los Angeles. They analysed the problem of dilution in a rising plume of sewage based on the earlier experiments conducted by Rawn and Palmer (1930). Utilizing dimensional analysis, they arrived at relationships in terms of dimensionless parameters. However, they did not study quantitatively in any detail the problem of a rising jet of sewage in stratified sea water.

Using data on coliform counts at outfalls discharging domestic sewage and a trial-and-error method of approximation, Pomeroy (1960) developed an empirical formula for determining the length of an ocean outfall required to keep the receiving waters within safe limits of bacterial contamination. Tests of the formula in a number of outfall designs gave good agreement between actual

coliform counts (when long-time averages of counts were taken) and predictions based on the formula.

Giving consideration to the problem of stratification in receiving sea water, Rawn *et al.* (1960) stated that if ρ_w is the density of waste and ρ_s and ρ_d are densities of the surface and deep sea water, respectively, the mixture of sea water and effluent will stay submerged below the surface layer if

$$\frac{(D-1)\,\rho_d + \rho_w}{D} > \rho_s$$

where D is the initial dilution as a ratio of sea water to waste. If the momentum of the rising column is sufficiently high, the effluent–seawater mixture can still break through the pycnocline and appear at the surface in a "boil". However, unless it becomes further diluted by a great deal of low-density water, the effluent mixture will sink at the periphery of the "boil" to the level where it meets water equal to its own denstiy. If the density of the rising mixture is sufficiently greater than the overlying layer to overcome the residual inertia of the rising column, the effluent will not appear at the surface.

Brooks (MS, 1963) demonstrated a procedure, based on an analysis by Morton *et al.* (1956), for evaluating the limiting height of a buoyant plume in a stratified aquatic environment. His formula, however, only applies to the case of a vertical jet with no momentum. Moreover, effects of ocean currents and of major changes in the marine environment due to the waste discharge were not taken into consideration. Nevertheless, a number of field checks has shown that the formula gives reasonable answers, its limitations notwithstanding.

The work described here shows that there can be a rather delicate balance between the density of the emerging mixture of effluent and sea water, at the surface above the outfall, and the density of the surface sea water. While the former remains comparatively uniform because of relatively unchanging salinity in the deep water, the latter undergoes large fluctuations with changes in runoff and air temperature. Consequently, the depth at which the field of effluent spreads varies with changing temperature and particularly salinity, which is the principal property effecting changes in density in Stuart Channel. Although it has been shown that the effluent field may form at the surface in the presence of comparatively high surface-water density, the high concentrations of effluent appear to be normally confined to thin layers at a depth of from 3 to 10 m. Under no circumstances has it been found that the effluent–seawater mixture sinks below the pycnocline (inflexion of the density vs. depth curve).

From design criteria established by other investigators (Pearson, 1956; Rawn *et al.*, 1960), it can be shown that higher initial dilution could be achieved at the pulpmill outfall in Stuart Channel by the following changes: (1) extend the pipe-line to a greater depth; (2) lengthen the diffuser in line or in a number of branches; (3) set the ports for more nearly horizontal discharge; (4) decrease the size of the ports and increase their number to an optimum; (5) spread the ports apart with intervals of at least 10 port diameters between them, to reduce interaction of rising plumes of effluent from individual discharge jets; and (6)

reduce the size of the end opening in the diffuser pipe or cap the end with a bulkhead (having a small porthole) which can be removed for cleaning.

Velocity of effluent flow through the diffuser barrel should be high enough to prevent deposition of settleable solids. With a long diffuser on a steeply-sloping bottom, it is desirable to grade the diameter of the ports to allow a greater discharge of effluent through the deeper ports than the upper ones and thus prevent clogging by deposition near the end of the diffuser. A good rule of thumb, established by design engineers (Rawn *et al.*, 1960) for multiple-port diffusers, is that the sum of all the port areas should be less than the cross-sectional area of the outfall pipe. On this basis, with a diameter of the diffuser pipe at 42 inches (107 cm) and ports of 6 inches (15.2 cm) diameter in the present pulpmill outfall, there should be ideally no more than 49 ports. According to the design plans for this diffuser, there are actually 20 ports, which together with the end opening give a discharge area of 1258 inches^2 (8117 cm^2) compared to 1385 inches^2 (8938 cm^2) for the cross-sectional area of the diffuser pipe. While this meets the above-stated criterion, the half-open end of the pipe considerably reduces the effectiveness of the ports in dispersion.

The entire behaviour of the effluent after it is discharged into a stratified environment is largely dependent on the fluid dynamics of the diffusion structure. Quantitative evaluation of parameters for submarine waste disposal into stratified waters using different outfall systems would be desirable, but it is beyond the scope of the research reported here. Ideally, one should carry out measurements at the outfall in Stuart Channel with variable flows from the pulp mill. This is hardly feasible under conditions of normal operation in the mill.

SUMMARY AND CONCLUSIONS

Since 1958, a 500-ton/day pulp mill at Crofton, B.C., has been discharging about 32 million US gal/day (49.5 cfs or 1.40 m^3/sec) of effluent into Stuart Channel by a 5000-ft (1.5-km) pipe-line terminating in a section with a series of openings (diffuser) at a depth of 10 fm (18 m) below low water. Oceanographic observations have been conducted in Stuart Channel since 1954 in order to evaluate the conditions prior to pulpmill installation and following.

Stuart Channel is a typical coastal estuarine region, with a stratified density structure resulting from moderately low salinities in the surface layer. Tidal currents may reach 1 kt (51 cm/sec) at the surface, but are usually an average maximum of less than 0.5 kt (20–25 cm/sec) at 5 m. At depths between 10 and 20 m, the currents are even weaker with maxima of 10–20 cm/sec. Currents at all depths observed near the Shoal Islands set to the northwest on the flood and to the southeast on the ebb, except at the surface, where they are apparently directed more to the southwest on the falling tide. From current observations in July 1957 near the proposed pulpmill outfall, net (non-tidal) currents were 8.7 cm/sec to the southwest at the surface; 6.2 cm/sec to the northwest at 4.6 m, 2.7 cm/sec to the southeast at 9.1 m and 1.1 cm/sec to the northwest at 18.3 m.

The pulpmill effluent entrains sea water by aspirator action as it rises with considerable force from the diffuser to the sea surface. Dilution generally averages about 1:22 (effluent:seawater) during the ascent. Under normal conditions, the effluent–seawater mixture is denser than the surface water in the channel and sinks to a depth of 3–10 m. Thereafter, it spreads with the prevailing currents in a thin field below the surface. This behaviour has been recognized from determinations of KME distribution and confirmed with dye-tracer experiments and *in-situ* transparency measurements. During some periods when salinity of the surface water is relatively high, the effluent–seawater mixture from the "boil" may spread over the surface of the channel. Different density profiles are shown as examples of conditions for surface and subsurface spread of effluent. The rapid seaward flushing through Sansum Narrows would be expected to occur when the effluent is confined to a thin surface layer or at a depth of around 9 m, where the net currents set to the southeast.

Dissolved oxygen concentrations in Stuart Channel have not been seriously impaired, but there has been some indication of a reduction in dissolved oxygen at the depth of maximum effluent concentration.

The major objectives in the installation of the submarine outfall with diffuser appear to have been generally achieved, *viz.* (1) discharge of the effluent as far seaward of the oyster leases on the Shoal Islands as economically practical; (2) a substantial initial dilution at the outfall; (3) dispersion of the effluent by the prevailing tidal flow in Stuart Channel; and (4) prevention of high concentrations of harmful substances in the surface water, particularly on the oyster leases. However, in the light of recent developments in diffuser design, certain improvements could be made which would increase the efficiency in dilution and dispersal from the outfall system.

Because of the tendency for the surface flow from the outfall area to be directed toward the southwest on the ebb tide, as shown both in current observations at an anchor station near the site of the diffuser and in aerial photographs, higher-than-average concentrations of KME may occasionally reach the oyster grounds on the southern island of the Shoal Island group. Although there was no clear evidence of such high concentrations from the available data, they could conceivably occur when the density of the surface sea water in Stuart Channel is high and winds blow from the east and southeast.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the willing co-operation of the officers and crew of CNAV *Ehkoli* and C.G.S. *A. P. Knight* throughout the field work for this project. British Columbia Forest Products Ltd. freely provided information on production and samples whenever requested. Messrs B. J. Burns, J. G. Varsanyi, J. R. Markert, S. Y. C. Mak, A. E. Werner, and J. H. Meikle provided technical assistance throughout the program. Dr D. B. Quayle and his assistants collected the water samples from selected points at approximately

monthly intervals for KME and salinity determination. The Surveys and Mapping Branch of the Provincial Department of Lands, Forests and Water Resources, Victoria, kindly made available the aerial photograph of Stuart Channel reproduced in this paper. In studying the background literature on the application of submarine diffusers, we were favoured by copies of unpublished manuscripts, and other information pertaining to the problem, from Dr N. H. Brooks of the California Institute of Technology, to whom we are extremely grateful.

REFERENCES

BARNES, C. A., E. E. COLLIAS, V. F. FELICETTA, O. GOLDSCHMID, B. F. HRUTFIORD, A. LIVINGSTON, J. L. MCCARTHY, G. L. TOOMBS, M. WALDICHUK AND R. WESTLEY. 1963. A standardized Pearl-Benson, or nitroso, method recommended for estimation of spent sulfite liquor or sulfite waste liquor concentration in waters. *Tappi*, **46**(6): 347–351.

BROOKS, N. H. 1960. Diffusion of sewage effluent in an ocean current, pp. 246–267. *In* E. A. Pearson, [Ed.], Proceedings First International Conference on Waste Disposal in the Marine Environment. Pergamon Press, Inc., New York, 569 pp.

MS, 1963. Limiting height of rise of a buoyant plume in a stratified environment. W. M. Keck Laboratory of Hydraulics and Water Resources, Division of Engineering and Applied Science, Calif. Inst. Technology, Tech. Memo. No. 63-6, 4 pp.

CALLAWAY, R. J. MS, 1963. Note on sulfite waste liquor and dissolved oxygen concentrations in the vicinity of a submarine outfall. U. S. Public Health Service, Portland, Oregon, 8 pp.

ELDRIDGE, E. F., AND G. T. ORLOB. 1951. Investigations of pollution of Port Gardner Bay and Snohomish River Estuary. *Sewage Ind. Wastes*, **23**(6): 782–795.

GUNNERSON, C. G. 1959. Sewage disposal in Santa Monica Bay. *Trans. Am. Soc. Civil Eng.*, **124**(No. 3002): 823–851.

1960. Discussion on "Eddy diffusion in homogeneous turbulence" by G. T. Orlob. *Proc. Am. Soc. Civil Eng.*, **85**(No. HY4): 101–109.

MORTON, B. R., G. I. TAYLOR AND J. S. TURNER. 1956. Turbulent gravitational convection from maintained sources. *Proc. Roy. Soc.*, Ser. A, **234**: 1–23.

OKUBO, AKIRA. 1962. A review of theoretical models for turbulent diffusion in the sea. *J. Oceanogr. Soc. Japan* (20th Anniv. Volume), pp. 286–320.

ORLOB, G. T., D. R. PETERSON AND K. R. JONES. 1951. A reinvestigation of pollution in Port Gardner Bay and the Lower Snohomish River. *Washington Pollution Control Comm. Tech. Bull.* No. 11, 11 pp.

PEARSON, E. A. 1956. An investigation of the efficacy of submarine outfall disposal of sewage and sludge. *State Water Pollution Control Board, Publ.* No. 14, 154 pp. Sacramento, Calif.

POMEROY, RICHARD. 1960. The empirical approach for determining the required length of ocean outfall, pp. 268–278. *In* E. A. Pearson, [ed.] Proceedings First International Conference on Waste Disposal in the Marine Environment. Pergamon Press, Inc., New York, 569 pp.

QUAYLE, D. B. MS, 1964. The effect of kraft mill effluent on the Pacific oyster (*Crassostrea gigas*) with particular reference to Crofton, B.C. *Fish. Res. Bd. Canada, MS Rept. (Biol.)*, No. 765, 30 pp.

RAWN, A. M., AND H. K. PALMER. 1930. Pre-determining the extent of a sewage field in sea water. *Trans. Am. Soc. Civil Eng.*, **94**(No. 1750): 1036–1081.

RAWN, A. M., F. R. BOWERMAN AND N. H. BROOKS. 1960. Diffusers for disposal of sewage in sea water. *Proc. Am. Soc. Civil Eng.*, **86**(No. SA 2): 65–105.

SHAW, A. E. MS, 1956. A proposal for more efficient effluent disposal in the sea. U.K. Atomic Energy Authority, Industrial Group, Rept. No. IGR–TN/D 396, 5 pp. Risley, Lancashire.

MS, 1957. Factors affecting the distance of discharge point from the shore in the sea disposal of effluent. *Ibid.*, Rept. No. IGR–TN/D 443, 11 pp.

WALDICHUK, M. MS, 1954. Pulpmill pollution problem in Osborn Bay, B.C. Fish. Res. Bd. Canada, Biological Station, Nanaimo, B.C. 11 pp.

1955. Effluent disposal from a proposed pulp mill at Crofton, B.C. *Fish. Res. Bd. Canada, Pacific Prog. Rept.*, No. 102, pp. 6–9.

1958. Summer oceanography in Osborn Bay, B.C. *Ibid.*, No. 110, pp. 6–12.

MS, 1964. Estimation of flushing rates from tide height and current data in an inshore marine channel of the Canadian Pacific Coast. Prepared for 2nd International Conference on Water Pollution Research, Tokyo, Japan, August 1964, 18 pp.

NOTES

A Quantitative Estimate of the Number of Pacific Herring in a Spawning Population

The British Columbia winter herring fishery depends on dense schools congregated in inshore waters. Shortly after the close of the fishery in early spring the herring spawn, depositing their adhesive eggs mainly on seaweeds in the intertidal zone. The length and width of individual spawnings can be readily measured at low tide, a routine procedure undertaken annually by officers of the Department of Fisheries of Canada. The intensity of deposition is also assessed, as one of five arbitrary categories — very light, light, medium, heavy, and very heavy — based on the number of eggs per-unit-area of substrate. By assigning these categories numerical weights from 1 to 5, respectively, the amount of spawn in any category can be converted to an equivalent length at a standard intensity of medium (a weight of 3).

In 1960, Fisheries Research Board of Canada personnel and officers of the Department of Fisheries of Canada made careful length and width measurements (Table I) on four spawnings in Area 17A (Fig. 1) in the lower east coast of Vancouver Island subdistrict. In addition, 125 sixteen-square-inch samples of spawn-laden vegetation were taken to determine the intensity of deposition.

TABLE I. Measurements of spawn abundance in Area 17A in 1960.

Spawning ground	Dimensions of spawning zone		Length (in statutory miles at a standard intensity of medium)
	Length (*yd*)	Area (*sq yd*)	
Hammond Bay	3,000	103,500	1.9
Taylor Bay	550	16,500	0.3
Departure Bay	1,350	68,125	1.1
Nanoose Bay[a]	9,495	469,800	4.6
Total:			7.9

[a]Ten per cent was deducted from the measured lengths to compensate for the patchiness of the vegetation at Nanoose Bay, an adjustment not required in the other localities.

The eggs in the samples were separated from each other and from the substrate by partial digestion of the outer membrane by 1*N* solution of potassium hydroxide for 30 min at 30°C. The detached eggs, carefully washed, were counted by a photo-electric impulse counter modelled after one described by

J. FISH. RES. BD. CANADA, 21(5), 1964.
Printed in Canada.

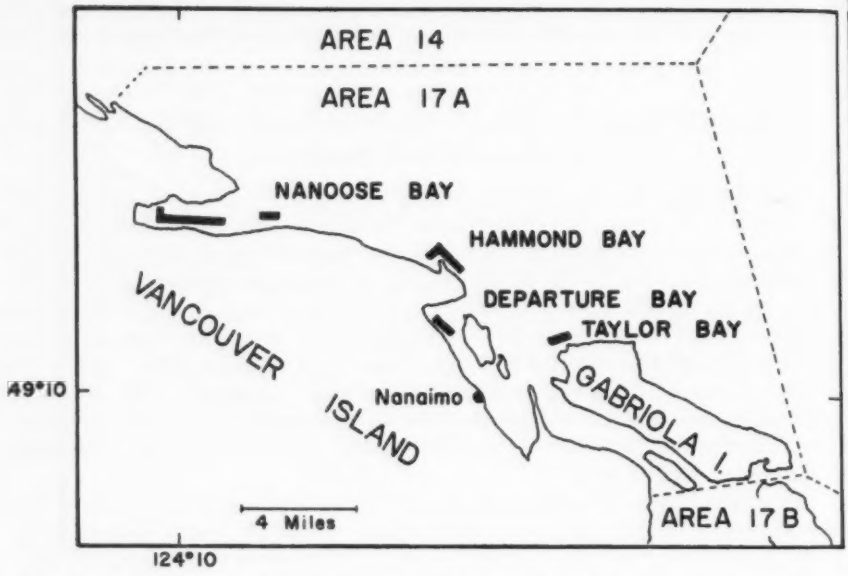


FIG. 1. The location of the four herring spawnings in Area 17A of the lower east coast of Vancouver Island subdistrict.

Parrish *et al.* (1960). The mean number of eggs per 16-square-inch sample for each of the four spawn depositions is given in Table II together with the standard deviations, the standard errors of the means, and the 95% confidence limits.

Knowing the length and width of the spawning zone and the number of eggs deposited per-unit-area it is possible to calculate the quantity of eggs on each spawning ground and the total number of eggs deposited in Area 17A. Using the mean number of eggs per-unit-area in each spawning, the total quantity of

TABLE II. The mean number of eggs per 16-square-inch samples taken in 1960 from the four Area 17A spawnings with standard deviations, standard errors of the means, and the upper and lower 95% confidence limits.

Spawning ground	No. of samples	Mean no. of eggs	Standard deviation	Standard error of the mean	95% confidence limits	
					Upper	Lower
Hammond Bay	23	6,570	±5073	±1059	8,766	4,374
Taylor Bay	46	11,864	±4853	±716	13,306	10,422
Departure Bay	45	2,861	±1627	±243	3,854	2,374
Nanoose Bay	11	9,849	±2967	±899	11,852	7,846

eggs spawned was found to be 461.5×10^9. As is usually the case, the intensity of deposition in all four spawnings was uneven, resulting in considerable variation in the number of eggs per 16-square-inch sample. This variation resulted in rather wide 95% confidence limits, 563.6×10^9 and 362.3×10^9.

The number of herring spawning in Area 17A can be obtained from these estimates of the numbers of eggs deposited and from data on the average number of eggs per female of each age (Nagasaki, 1958), and on the age composition and percentage of mature females at each age (Table III) obtained from samples of the catch in the preceding winter fishery in Area 17A. In this way there were estimated to be about 59 million herring spawning in Area 17A in 1960. The upper and lower 95% confidence limits were 72 and 46 million. These estimates correspond to 6416, 7834, and 5036 tons of herring, respectively.

TABLE III. Per cent age composition, per cent mature females, number of eggs per female, and average weight of herring of each age in samples from the preceding Area 17A winter catch.

Age (years completed)	Per cent age composition	Per cent mature females	No. of eggs per female $\times 10^3$	Average weight (g)
0	–	–	–	–
1+	8.4	30	9.1	52
2+	48.2	42	14.8	91
3+	38.4	58	18.6	114
4+	4.4	42	21.3	128
5+	0.4	–	–	159
6+	–	–	–	–
7+	0.3	100	26.2	145

The four spawnings in Area 17A produced 7.9 miles of spawn of standard (medium) intensity. Thus about 7.5 million herring, with 95% confidence limits of 5.8 and 9.1 million, were required to deposit a mile of spawn of standard intensity. This estimate, although a little lower, does not compare unfavourably with two earlier estimates, one of 8 million spawners per mile of spawn (Hourston, 1953) for the northern population, the other of 9 million per mile of spawn (Stevenson and Outram, 1953) for the lower east coast of Vancouver Island population. Hourston's estimate was derived from echo-sounding surveys of spawning schools, and that of Stevenson and Outram from an analysis of qualitative changes in total population abundance from year to year.

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

D. N. OUTRAM
F. H. C. TAYLOR

Received for publication April 27, 1964.

REFERENCES

HOURSTON, A. S. 1953. Estimation of herring population size by means of echo-sounder tracings and its application to herring research. *Fish. Res. Bd. Canada, Nanaimo Biological Station Circular*, No. 26, 26 pp.

NAGASAKI, F. 1958. The fecundity of Pacific herring (*Clupea pallasii*) in British Columbia coastal waters. *J. Fish. Res. Bd. Canada*, **15**(3): 313–330.

PARRISH, B. B., I. G. BAXTER AND M. J. D. MOWAT. 1960. An automatic fish egg counter. *Nature*, **185**(4715), p. 777.

STEVENSON, J. C., AND D. N. OUTRAM. 1953. Results of investigation of the herring population on the west coast and lower east coast of Vancouver Island in 1952–53, with an analysis of fluctuation in population abundance since 1946–47. *Report British Columbia Fisheries Department* for 1952, pp. 57–84.

Occurrence and Distribution of Sea Water in Sakinaw Lake, British Columbia

Sakinaw Lake lies near the northern end of Sechelt Peninsula (Fig. 1) in a basin composed largely of batholithic rocks, mainly quartz diorites and granodiorites, but broken about halfway along its length by a narrow band of altered volcanic rocks (Bacon, 1957). The lake is over 8 km (5 miles) in length with a surface area of about 8 km² (2016 acres); it has a maximum depth of 140 m (460 ft) and a mean depth of 43 m (140 ft). Its tributaries include a number of small streams and lakes as well as Ruby Lake with a maximum depth of 112 m (366 ft).

Sakinaw Lake lies about 5 m above lowest normal tide level. The exact elevation of Sakinaw Lake is not known but it is between 2.7 and 3.9 m above mean sea level (personal communication, J. H. Doughty-Davies, B. C. Water Investigations Branch). The lake outlet has been partially or completely blocked by dams built for logging purposes since the early 1900's. A permanent dam and fishway was constructed on the outlet late in 1952 by the Department of Fisheries of Canada and has been regulated since then to prevent entry of water with tides below 5 m (16 ft) height.

A brief examination of temperature and salinity conditions was made on Sakinaw Lake early in 1948 by Dr J. P. Tully. His observations were limited to the upper 10 m and did not record any evidence of sea water. On May 23, 1959, a Fish and Game Branch survey crew made 31 transects of the lake with a recording echo sounder to obtain the morphometric features shown in Fig. 1.

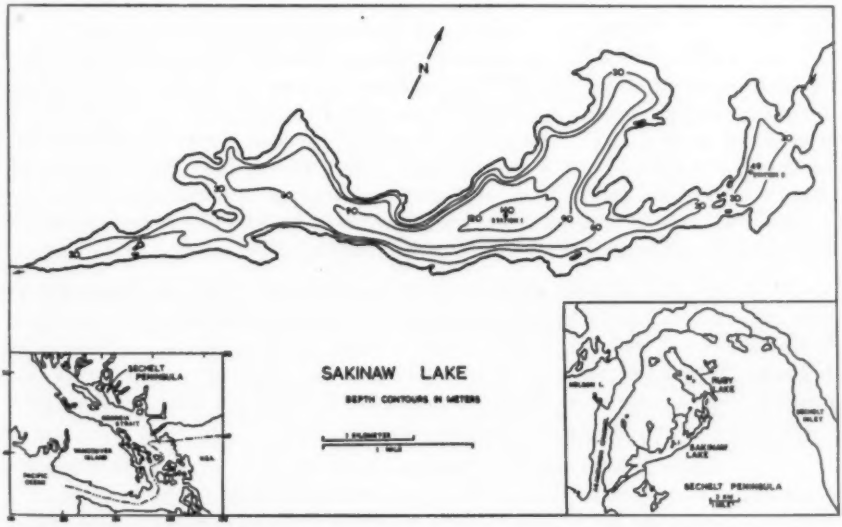


FIG. 1. Geographic and morphometric features of Sakinaw Lake, British Columbia.

J. FISH. RES. BD. CANADA, 21(5), 1964.
Printed in Canada.

In addition a surface water sample was analysed for total dissolved solid content (113 ppm), and plankton hauls and gill net sets were made. In April 1960, biologists from the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C., visited the lake and took temperature and salinity measurements to a depth of nearly 80 m at Station 1. These demonstrated a marked increase in temperature and salinity below a depth of 30 m (Fig. 2). More complete

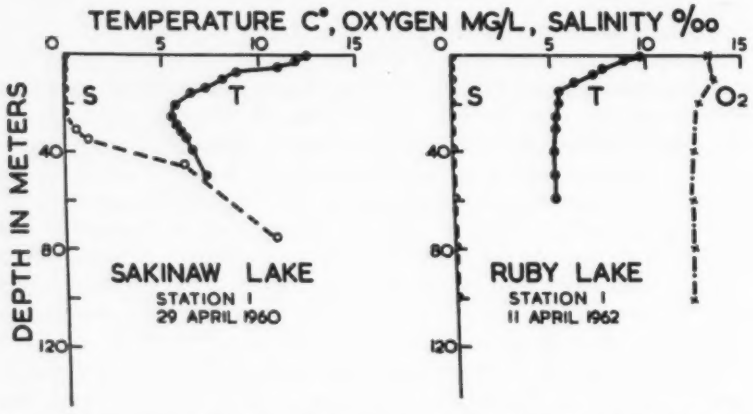


FIG. 2. Temperature, salinity, and dissolved oxygen profiles for Sakinaw and Ruby Lakes, British Columbia.

physical and chemical observations made by the Fish and Game Branch in 1962 are shown in Fig. 3.

At Station 1 a rapid temperature increase occurred between 30 and 60 m on both sampling dates. Similarly a marked increase in salinity (silver nitrate titration with no correction for H_2S or unusual ionic balance) and conductivity was noted in this layer. Below 60 m salinity showed little further increase, attaining a maximum value slightly over 11‰. Dissolved oxygen content fell sharply at depths below 20 m and was not detected by unmodified Winkler analysis below 30 m. A strong H_2S smell was evident in all water samples below 30 m and those below 60 m exhibited strong frothing when brought to the surface.

Although the separate depression at the northeast end of the lake extends well below 30 m (Fig. 1), there is no evidence of sea water intrusion into this basin from its thermal, salinity, or conductivity characteristics (Fig. 3, — Station 2). Likewise Ruby Lake, lying at an elevation of about 18 m above Sakinaw Lake, does not contain any sea water in its basin(Fig. 2) and has a total dissolved solid content of 40 ppm, well below that for Sakinaw Lake.

There seems little doubt that Sakinaw Lake offers an example of ectogenic meromixis (Hutchinson, 1957). However, from the data at hand it is only possible to speculate as to the age of the sea water in its main basin. As opposed to nearby Powell Lake (Williams *et al.*, 1961), it appears to be, at least in part,

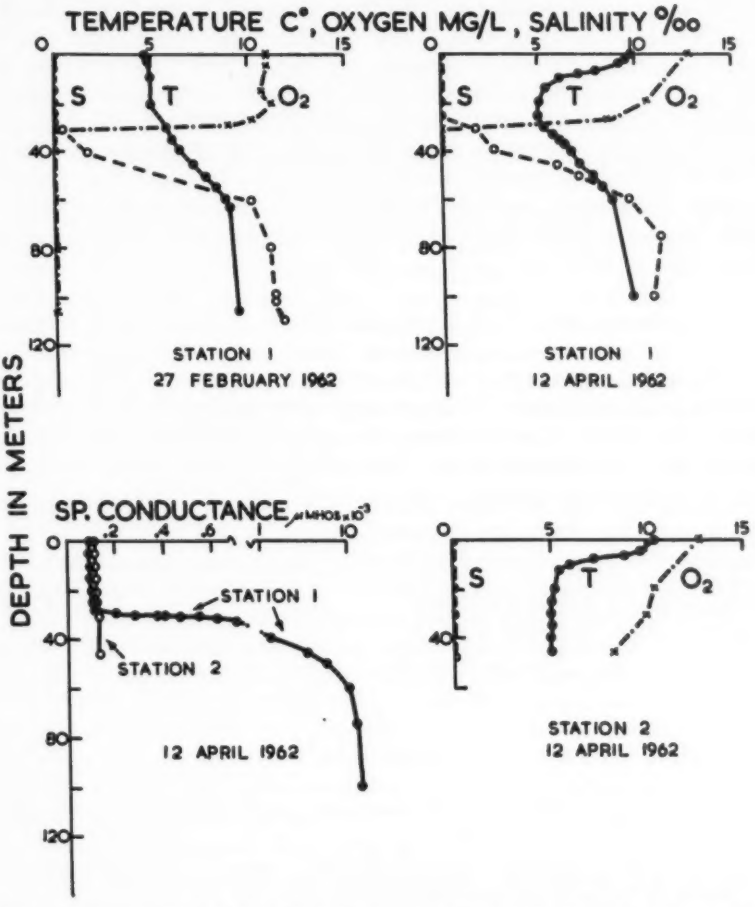


FIG. 3. Temperature, salinity, dissolved oxygen, and conductivity profiles for the two basins of Sakinaw Lake, British Columbia.

of rather recent origin. There were no doubt periodic intrusions of sea water prior to the existence of dams at the outlet, or possibly more recently under the right combination of wind and tide.

The higher total dissolved solid content of the surface waters of Sakinaw Lake (113 ppm), as compared with Ruby Lake (40 ppm), may be the result of addition to the mixolimnion from the saline monimolimnion through limited mixing.

If it can be established that the existing dam at the outlet prevents any further intrusion of sea water, this meromictic lake would be an excellent one in which to study conditions of freshening of the basin (Griesel, 1935).

The fauna of Sakinaw Lake contains characteristically freshwater as well as anadromous forms. Bosminids and daphnids were noted in the planktonic cladocerans, while *Diaptomus oregonensis* Lilljeborg and *Cyclops thomasi* S. A. Forbes are represented in the planktonic copepods. The mysid *Acanthomysis awatchensis* (Brandt) occurs in the lake. The fish fauna of Sakinaw Lake includes the coastal cutthroat trout *Salmo clarkii clarkii* Richardson, at least one species of salmon *Oncorhynchus nerka* (Walbaum), peamouth chub *Mylocheilus caurinum* (Richardson), and the prickly sculpin *Cottus asper* Richardson. The Pacific lamprey *Entosphenus tridentatus* (Gairdner) has been taken from Sakinaw Lake outlet.

The assistance of Mr J. S. Northcote who loaned his boat and participated in field work throughout a snowstorm on February 27, 1962, is sincerely appreciated. Messrs J. A. Balkwill, C. A. Gill and C. E. Stenton also helped in collection of field data. Dr Mildred S. Wilson kindly identified copepods from plankton samples. Dr G. L. Pickard arranged for salinity analysis at the Institute of Oceanography, University of British Columbia.

British Columbia Fish and Game Branch
Department of Recreation and Conservation
Vancouver, B.C. — T. G. NORTHCOTE

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C. — W. E. JOHNSON

Received for publication March 12, 1964.

REFERENCES

BACON, W. R. 1957. Geology of lower Jervis Inlet, British Columbia. *British Columbia Department Mines Bull.*, No. 39, 45 pp.

WILLIAMS, P. M., W. H. MATHEWS AND G. L. PICKARD. 1961. A lake in British Columbia containing old sea water. *Nature*, **191**: 830–832.

HUTCHINSON, G. EVELYN. 1957. A treatise on limnology, Vol. I. John Wiley & Sons, New York – London, 1015 pp.

GRIESEL, R. 1935. Die Aussüssung des Hemmelsdorfer Sees. *Mitt. Geogr. Ges. Lübeck*, 2 Reihe, **38**: 77–83.

Successful Introduction of *Mysis relicta* Lovén into Kootenay Lake, British Columbia

In 1939, W. A. Clemens suggested the introduction of *Mysis relicta* and *Pontoporeia affinis* into Okanagan Lake as a partial solution for fish cultural problems (Clemens *et al.*, 1939), and Waterton Lake, Alberta, was mentioned as a source of supply for the introduction. An investigation of Kootenay Lake in 1949 led to similar conclusions (Larkin, 1951) which can be generalized to many of the deep oligotrophic lakes west of the continental divide (Larkin, 1952). In Kootenay Lake, for example, rainbow trout undergo a marked change in diet after three years of age, shifting from predominantly terrestrial insects and small invertebrates to kokanee (*Oncorhynchus nerka* Walbaum) (Larkin *et al.*, 1957; Cartwright, 1961). *Mysis* and *Pontoporeia* would ostensibly provide a supplementary food source of large invertebrates to facilitate the change in diet of intermediate-sized trout.

Kootenay Lake lies in a deep glacial trench in southeastern British Columbia and is 154 square miles (399 sq km) in area with a maximum depth of 530 ft (161 m). In July and October of 1949, as well as June and September of 1950, *Pontoporeia affinis* and *Mysis relicta* from Upper Waterton Lake were collected by dragging a bottom trawl (Beauchamp, 1932) in 100 ft (30 m) of water. For the 300-mile (483 km) transfer to Kootenay Lake, the animals were transported in fry cans (500 per can) with iced lake water. Immediately prior to introductions, transport water was 8.9–12.2°C and lake water was 11.1–14.4°C. Approximately 25,000 *Mysis* and *Pontoporeia* were introduced into Kootenay Lake in the four transfers, about one-half of which were *Mysis*. The animals were introduced at three locations on Kootenay Lake (Fig. 1).

In the first decade after the introductions, no *Mysis* or *Pontoporeia* were observed either in the lake or in stomach contents of rainbow trout taken by anglers. Only occasional attempts were made to specifically look for the appearance of these invertebrates in numbers.

In late June of 1961 and again in 1962, *Mysis* were observed near the surface at Nine Mile Narrows in the west arm of Kootenay Lake (Fig. 1). Collections at Nine Mile Narrows at midday in late June of 1963 confirmed the observations of the two previous years.

Use of a tow-net, similar to that described by Johnson (1956), failed to locate *Mysis* by spot sampling in Crawford and Kaslo Bays (Fig. 1) in the late summer and fall of 1963, although the towing speed may have been inadequate with the mesh size used (5/32 inch). *Pontoporeia* and *Mysis* were not encountered in Ekman dredge bottom samples taken from parts of the north, south, or west arms of the lake.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

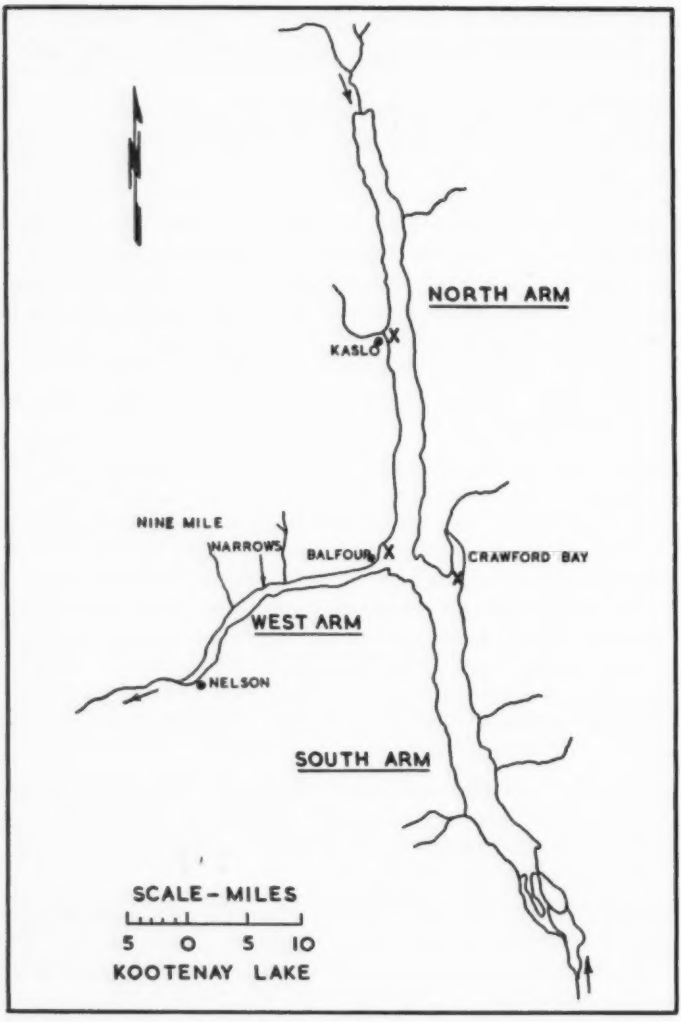


FIG. 1. Kootenay Lake with crosses indicating the location of *Mysis* introduction.

In the west arm, stomach samples from rainbow trout between 25 and 60 cm, Dolly Varden (*Salvelinus malma* Walbaum), kokanee and mountain whitefish (*Prosopium williamsoni* Girard) contained *Mysis*. *Mysis* have also been observed in Dolly Varden and rainbow trout up to 27 lb (12.2 kg), taken throughout most of the north arm. No stomach samples from fish in the south arm of Kootenay Lake have been examined.

Mysis thus seem to have been successfully introduced into Kootenay Lake. Preliminary observations suggest that there have been marked effects on the growth rate of rainbow trout and kokanee. Many specimens of the latter have been collected which exceeded 3 lb (1.4 kg), whereas in 1951, none were collected which exceeded ½ lb (250 g) (Vernon, 1957).

Fish and Game Branch
British Columbia Department of
Recreation and Conservation
Cranbrook, B.C.
R. A. H. SPARROW

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.
P. A. LARKIN

Fish and Game Branch
British Columbia Department of
Recreation and Conservation
Nelson, B.C.
R. A. RUTHERGLEN

REFERENCES

BEAUCHAMP, R. S. A. 1932. A new dredge. *Int. Rev. Hydrobiol.*, **27**: 467–479.

CARTWRIGHT, J. W. 1961. Investigation of the rainbow trout of Kootenay Lake, British Columbia, with special reference to the Lardeau River. *British Columbia Game Commission, Management Publ.*, No. 7, 46 pp.

CLEMENS, W. A., D. S. RAWSON, AND J. L. MCHUGH. 1939. A biological survey of Okanagan Lake, British Columbia. *Bull. Fish. Res. Bd. Canada*, No. 56, 70 pp.

JOHNSON, W. E. 1956. On the distribution of young sockeye salmon (*Oncorhynchus nerka*) in Babine and Nilkitkwa, B.C. *J. Fish. Res. Bd. Canada*, **13**(5): 695–708.

LARKIN, P. A. 1951. Summary of investigation conducted by the Fisheries Research Group, attached to the British Columbia Game Department, in 1949. *Annual Report of the British Columbia Game Commission* for 1949, pp. 55–61.

1952. The role of research in the management of fresh water fisheries in British Columbia. *Canadian Fish Culturist*, **12**: 10–12.

LARKIN, P. A., J. G. TERPENNING, AND R. R. PARKER. 1957. Size as a determinant of growth rate in rainbow trout *Salmo gairdneri*. *Trans. Amer. Fish. Soc.*, **86**: 84–96.

VERNON, E. H. 1957. Morphometric comparison of three races of kokanee (*Oncorhynchus nerka*) within a large British Columbia lake. *J. Fish. Res. Bd. Canada*, **14**(4): 573–598.

Further Information on Spawning Stock Size and Resultant Production for Skeena Sockeye

Shepard and Withler (1958) derived a reproduction curve showing the relationship between the abundance of spawners and resultant return of maturing age 4_2 and 5_2 sockeye (*Oncorhynchus nerka*) of the Skeena River. The curve, derived empirically from moving means of associated escapement–return values ranked in order of increasing escapements, was based on data for the 45-year period 1908 to 1952. The curve (Fig. 1) displayed an almost linear ascending limb and a very precipitous descending limb. Maximum production (2.4 million sockeye) was achieved at spawning levels of slightly over 0.9 million; maximum sustained yield (1.4 million) was provided by spawnings of 0.9 million.

Tanaka (1962) using the same data claimed that the relation between escapement and return had varied from period to period as a result, primarily, of changes in environmental conditions. As a consequence he considered that the use of a single curve relating escapement and return throughout the history of the fishery was inappropriate. Instead, he constructed a series of curves describing the relationship for series of years in which good, medium, and poor environmental conditions prevailed. Canadian authors (Anon., 1962), while recognizing that there were marked year to year variations, could find no evidence for such long-term trends in escapement and return generated by persistent changes in environmental conditions. They considered that it was most appropriate to fit the available data with a single empirical curve.

Since publication of the Shepard and Withler (1958) paper, escapement–return data have become available for an additional 6 brood years. These data (Table I) are plotted in Fig. 1 along with the original data (the trend line has not been altered to account for the position of the new points). In the past 6 years, two of the points represent rather extreme returns considering the numbers of spawners involved. The return from the 1957 spawning was very good — 2,179,000 or 1.8 times the return expected on the basis of the trend line. The return per spawner was the fourth greatest in the 51-year period of record, exceeded only by values for 1936, 1921, and 1932. In contrast, the total return from the 1958 brood was extremely poor — 799,000, less than enough to replace the parent escapement and only 0.4 times the expected return. Smolt output data for Babine Lake (supporting over 80% of the Skeena sockeye spawners during the 6-year period) indicate that the freshwater survival of the 1958 brood was not unusually low. The estimated numbers of smolts produced from this brood (57.2 million) was even greater than that estimated for the 1957 brood (33.9 million) which provided the excellent return noted above. Thus, it must be concluded that, for reasons unknown, the 1958 brood suffered an unusually great mortality at sea.

J. Fish. Res. Bd. Canada, 21(5), 1964.
Printed in Canada.

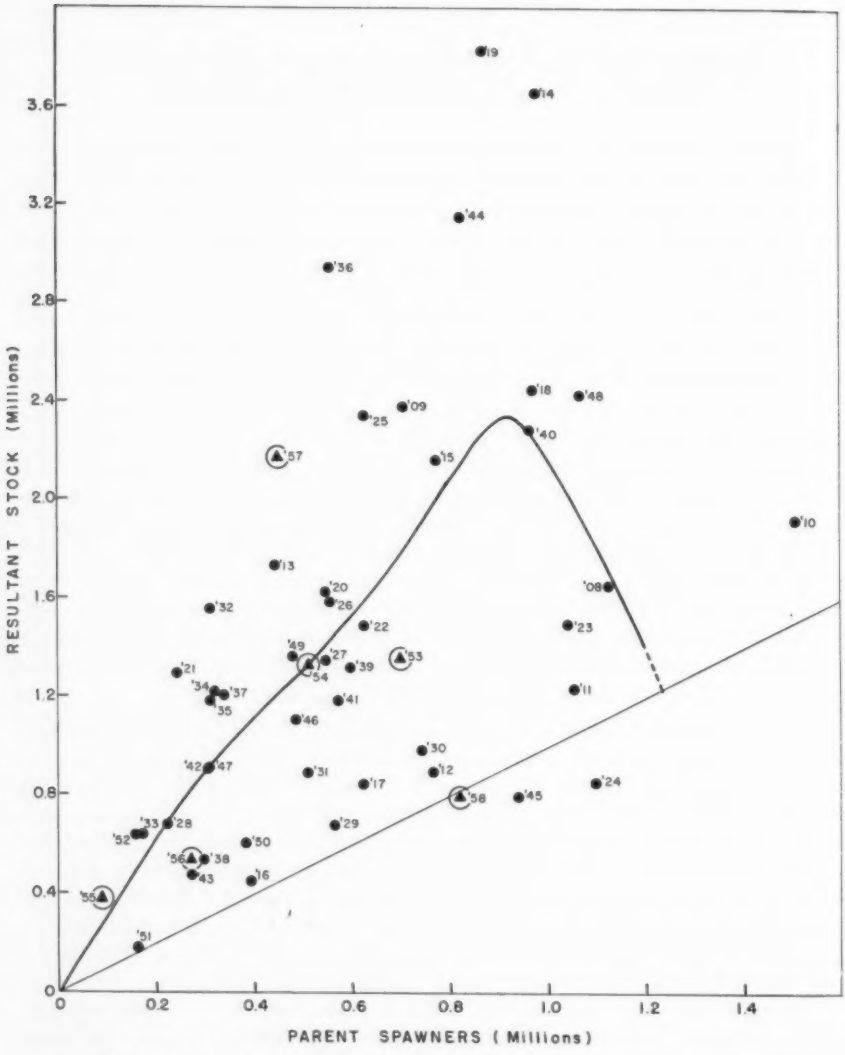


FIG. 1. Numbers of 4_2 and 5_3 Skeena sockeye (catch plus escapement) plotted against numbers of parent spawners. Figures in the body of the graph indicate brood years. Encircled points represent recent escapement–return values. (Data for the period 1908 to 1952 from Shepard and Withler, 1958.)

TABLE I. Estimates of parent spawners and resultant stock for Skeena 4_2 and 5_2 sockeye, 1953 to 1963.

I[a]	XIII[a]	XIV[a]	XV[a]	XVI[a]
Year	Spawning escapement	Resultant stock		
	Pn	4_2	5_2	Total *Sn*
		thousands of fish		
1953	700[b]	524	825	1,349
1954	511[b]	654	671	1,325
1955	87[b]	252	127	379
1956	370[b]	307	233	540
1957	448	1,569	610	2,179
1958	819	418	381	799
1959	799	357	...	...
1960	273	...	...	...
1961	984	...	...	...
1962	558	...	...	...
1963	609	...	...	...

[a]Column numbers are the same as those in table I of Shepard and Withler (1958).

[b]Re-analysis of escapement data has resulted in some changes in the values presented in column XIII of table I of Shepard and Withler (1958).

The recent data obviously lend no support to Tanaka's hypothesis of a sequence of levels of productivity. In the short space of 6 years the observed returns span the extreme range of the three levels he postulated.

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

M. P. SHEPARD
F. C. WITHLER
J. MCDONALD
K. V. ARO

Received for publication April 27, 1964.

REFERENCES

ANON. 1962. Biological Station, Nanaimo, B.C. *Fish. Res. Bd. Canada, Ann. Rept.* for 1961–62, pp. 95–129.

1962. Further considerations on the status of the sockeye stocks of the Fraser and Skeena River systems with respect to Articles III(1)(a) and IV of the International Convention for the High Seas Fisheries of the North Pacific Ocean. *Bull. Int. North Pacific Fisheries Comm.*, **9**: 91–105.

SHEPARD, M. P., AND F. C. WITHLER. 1958. Spawning stock size and resultant production for Skeena sockeye. *J. Fish. Res. Bd. Canada*, **15**: 1007–1025.

TANAKA, S. 1962. On the salmon stocks of the Pacific coast of the United States and Canada (views of the Japanese national section on the abstention cases of the United States and Canada). *Bull. Int. North Pacific Fisheries Comm.*, **9**: 69–84.

Contribution to the Marine Life History of the Eulachon *Thaleichthys pacificus*

Little is known about the distribution of eulachon from the time the larvae leave the rivers until the time the adults return to spawn. In British Columbia, spawning usually occurs during March and April in the larger mainland rivers and some of the smaller streams. The slender, transparent, newly hatched larvae are about 4–5 mm long. They are feeble swimmers, and in the Fraser River they are apparently carried to sea soon after emerging from the egg (Hart and McHugh, 1944). Larvae from the spawning areas of the Columbia River have been traced in their downstream drift to within 20 miles of the sea (Smith and Saalfeld, 1955). Records of field observations kept at the Biological Station, Nanaimo, B.C., show that adult eulachon have been found in the stomachs of many species of fish including dogfish, salmon, hake, Pacific cod, and lingcod, as well as marine mammals such as harbour seals and fur seals. Their relative importance in the diet of both fish and mammals is not known.

Collections from the echo scattering layers in the coastal waters of British Columbia have yielded new data on the distribution of the eulachon. Larval, juvenile, and adult life-history stages have been collected from catches made at various depths with midwater trawl gear. Data on the size of eulachon captured in midwater trawls and shrimp trawls in 1963 and in previous years are given in Table I. A tentative assignment of ages has been made on the basis of length–frequency distributions (Fig. 1). The data to support the assignment of ages shown in Fig. 1 have been plotted from fork lengths summarized in Table I. Although these data were collected in different years and from widely scattered areas along the British Columbia coast, the broken line connecting the mean lengths of the different samples tends to support the age-group assignment.

Larvae and fry of age-group 0+ are still semi-transparent (Fig. 2). The black eyes are a pronounced feature of the head. In larvae measuring 18–32 mm fork length, there is a distinctive row of small, black melanophores along the ventral edge of each side of the abdomen and of the body above the anal fin. In age-group 0+ fry measuring 46–51 mm fork length caught in December, the melanophores are confined to the region above the anal fin. The caudal fin and dorsal surface of the body of these larger fry are sparsely covered with a stippling of very small melanophores. The peritoneum is densely lined with small black pigment cells. The typical adult pigmentation seemed to be complete in juvenile fish completing their second year of life (age 1+).

The first indication of maturing gonads was noted in fish of age-group 2+, caught in the late summer and winter months. Eulachon thus do not spawn for the first time until they are 3 years of age. This is additional evidence establishing the age of maturity. The parent–progeny relationship of eulachon in the Fraser River, investigated by Ricker *et al.* (MS, 1954), was based on the

J. Fish. Res. Bd. Canada, **21**(5), 1964.
Printed in Canada.

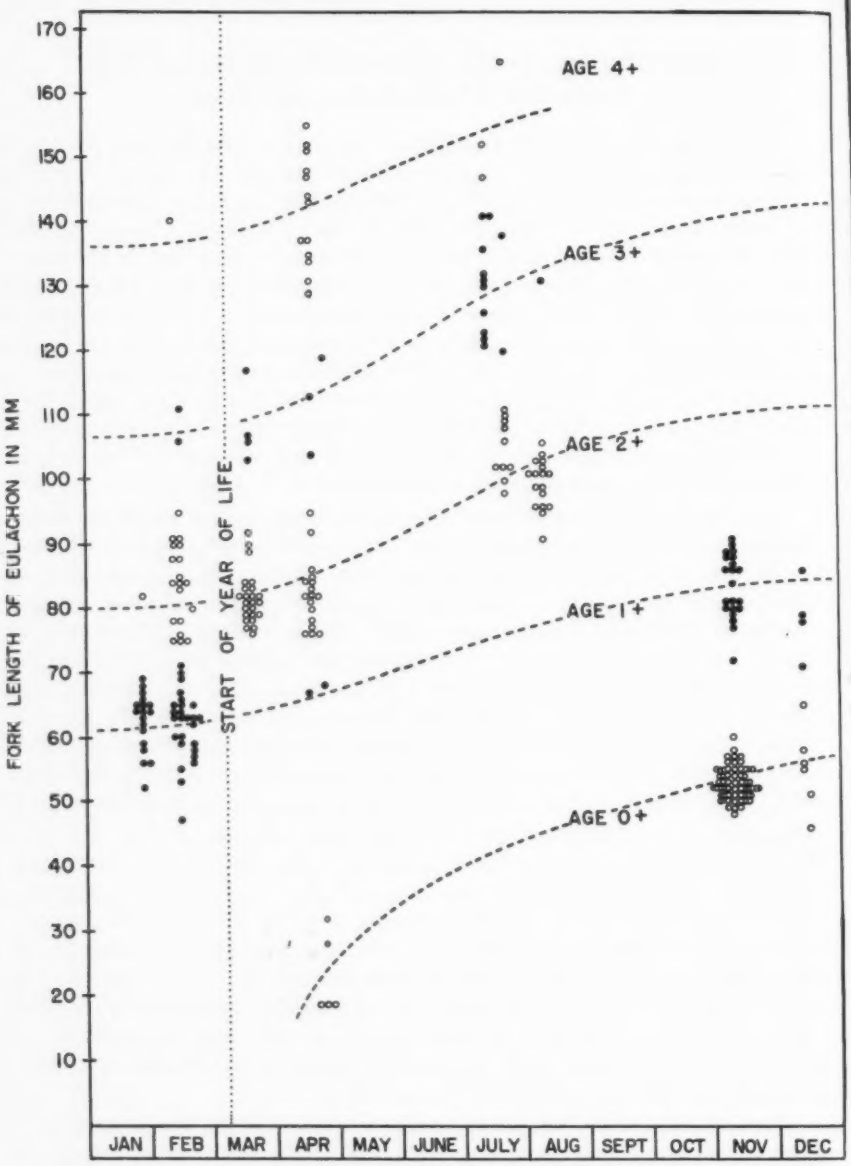


FIG. 1. Length–frequency distribution of samples of eulachon *Thaleichthys pacificus* taken in various seasons of the year.

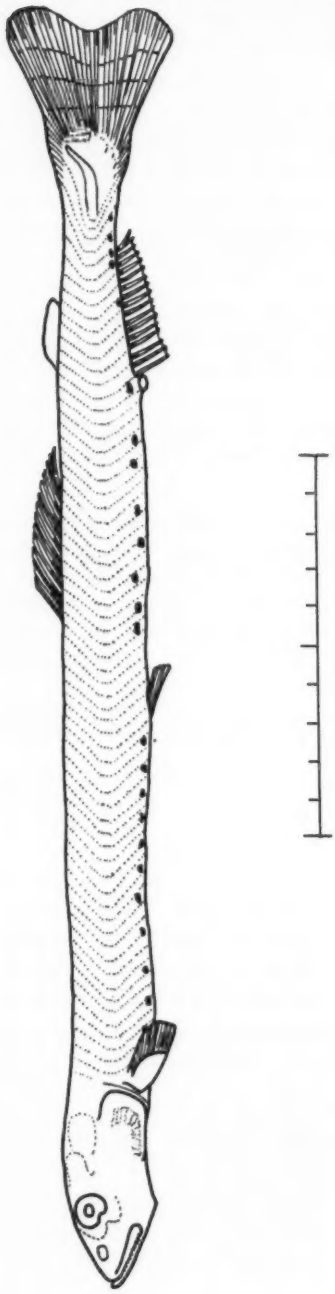


FIG. 2. Larval eulachon *Thaleichthys pacificus* caught off Race Rocks in Juan de Fuca Strait.

TABLE I. The range in length and the mean length of eulachon taken in various midwater and shrimp trawls in British Columbia.

Location	Date	Depth	Gear	Age	No. fish examined	Total length		Fork length		Standard length	
						Size range	Mean	Size range	Mean	Size range	Mean
		fm				*mm*	*mm*	*mm*	*mm*	*mm*	*mm*
Fraser River	March–April		MWT[a] ST[b]	0+	...	Newly hatched, about 5 mm					
Juan de Fuca Strait, Race Rocks	April 23, 1963	15	MWT	0+	5	18–34	24	18–32	23	17–30	21
Haro Strait	April 23, 1963	35	MWT	1+	1	...	75	...	68	...	60
				3+	1	...	131	...	119	...	107
Strait of Georgia	April 2, 1957	40–60	ST	1+	1	...	...	...	66	...	60
				2+	16	77–100	87	72–92	82	64–80	70
				3+	2	112–123	117	104–113	108	91–101	96
				4+	13	140–170	154	129–155	142	114–135	126
Dixon Entrance off Argonaut Hill, Queen Charlotte Islands	July 11, 1954	90	ST	3+	10	...	...	121–141	130	...	...
				4+	2	...	...	143–152	147	...	...
Hecate Strait off Rose Spit, Queen Charlotte Islands	July 19, 1953	14–18	ST	2+	10	...	...	98–111	105	...	...
				3+	3	...	...	120–144	134	...	...
				5+	1	...	...	...	165	...	...
Mouth of Sydney Inlet, west coast Vancouver Island	Aug. 7, 1952	12	ST	2+	17	99–114	108	91–106	100	83–95	90
				3+	1	...	144	...	131	...	120
Malacca Passage, Chatham Sound	Nov. 7, 1963	50	MWT	0+	61	...	...	48–60	53	...	...
				1+	21	...	...	72–91	83	...	...
Off Entrance Island, Strait of Georgia	Dec. 13, 1963	105	ST	0+	4	59–69	63	55–65	58	49–56	52
				1+	4	77–94	86	71–86	78	64–77	70
Off Ballenas Islands, Strait of Georgia	Dec. 13, 1962	80	MWT	0+	2	52–55	53	46–51	48	41–45	43
Saanich Inlet, east coast Vancouver Island	Jan. 30, 1962	48	MWT	0+	18	57–75	68	52–69	62	47–60	55
				1+	1	...	90	...	82	...	74
Satellite Channel, east coast Vancouver Island	Feb. 12, 1963	30	MWT	0+	12	64–77	69	59–71	64	53–64	52
				1+	17	80–105	91	73–95	84	65–85	75
				2+	1	...	122	...	111	...	100
Saanich Inlet, east coast Vancouver Island	Feb. 12–14/63	41–55	MWT	0+	6	50–74	64	47–67	59	42–60	53
				1+	1	...	93	...	85	...	76
				2+	1	...	118	...	106	...	96
				4+	1	...	152	...	140	...	125
Off Ballenas Islands, east coast Vancouver Island	Feb. 19, 1963	54–85	MWT	0+	9	61–69	65	56–65	61	50–59	55
				1+	1	...	85	...	80	...	71

[a]Midwater trawl.
[b]Shrimp trawl.

premise that most fish matured at 2+ years. They noted that their analysis would need revision if the maturity at age 2 was inaccurate.

Of particular interest is the coastal distribution of juvenile eulachon during their first 2 years of life in the sea. The wide distribution of eulachon in their first year of life in the Strait of Georgia is probably the result of the dispersion of larvae from the Fraser River by the general counterclockwise circulation of water in the Strait. The occurrence of larval fish (23 mm fork length) off Race Rocks in April may be attributed to the rapid spring flushing of the newly hatched larvae from the Fraser River, and their direct transport by the surface water runoff across the Strait of Georgia. Evidence of this rapid flushing is seen in the lower salinities in the surface layer in the southern Strait of Georgia during the spring season (Anon. 1946–1960; Hollister, MS, 1960–1962). The capture of larval and juvenile eulachon in the echo scattering layers in coastal waters at various seasons of the year suggests that they spend a considerable portion of their first 2 years of life in the sea in these food-rich zones. The stomachs of juveniles were found to contain chiefly euphausiids which are very abundant in these echo scattering layers.

Many adult eulachon are found dead in the Fraser and Columbia Rivers at the time of spawning, and on the basis of this and other available evidence it has been assumed that most eulachon die after spawning. However, spent eulachon in good condition caught by trawlers in the Strait of Georgia off the mouth of the Fraser River suggest that some eulachon recover after spawning, and may spawn a second time.

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C. .

W. E. BARRACLOUGH

Received for publication June 2, 1964.

REFERENCES

ANON. 1946–1960. Pacific Drainage. *Canada Department of Northern Affairs and National Resources, Water Resources Branch, Water Resources Papers*, Nos. 106 to 131.

HART, JOHN LAWSON, AND J. LAURENCE MCHUGH. 1944. The smelts (Osmeridae) of British Columbia. *Bull. Fish. Res. Bd. Canada*, No. 64, 27 pp.

HOLLISTER, H. J. MS, 1960–1962. Observations of seawater temperature and salinity on the Pacific coast of Canada, Vols. XIX, XX, XXI. *Fish. Res. Bd. Canada, MS Rept. (Oceanogr. and Limnol.)*, Nos. 67, 104, 131.

RICKER, W. E., DOROTHY FURK MANZER AND ELIZABETH A. NEAVE. MS, 1954. The Frase River eulachon fishery, 1941–1953. *Fish. Res. Bd. Canada, MS Rept. Biol. Sta.*, No.583 35 pp.

SMITH, WENDELL E., AND ROBERT W. SAALFELD. 1955. Studies on Columbia River smelt *Thaleichthys pacificus* (Richardson). *Fish. Res. Papers, Washington Dept. Fish.*, **1**(3): 3–26.

[a]Midwater trawl.
[b]Shrimp trawl.

Distinguishing Characters for the Sculpins *Cottus bairdii* and *C. cognatus* in Eastern Canada

Identification of specimens[1] of the mottled sculpin, *Cottus bairdii* Girard, and the slimy sculpin, *Cottus cognatus* Richardson, has been difficult because of the variability of the known distinguishing characters. The two species are quite closely related, both belonging in the *bairdii* species group (McAllister and Lindsey, 1961; Bailey and Bond, 1963). None of the characters previously employed would separate all specimens.

A collection of 130 specimens (all over 40 mm in standard length) of these two species from Ontario and Quebec was studied in an effort to find a diagnostic character that would separate all specimens. Methods of measuring and counting are indicated in Fig. 1 and footnotes to Table I.

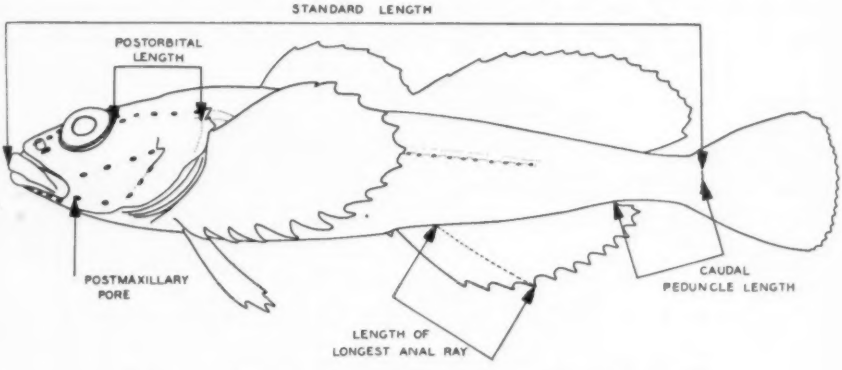


FIG. 1. Methods of measurement and position of postmaxillary pores.

[1]The following specimens in the National Museum of Canada were examined:

Cottus bairdii: NMC60-252: Ste. Foy, P.Q. (1 specimen); NMC58-313: Cesarea, Ont. (1); NMC59-41: Ottawa, Ont. (1); NMC58-254: Gatineau Valley, P.Q. (1); NMC58-204: Ottawa, Ont. (2); NMC59-40: Ottawa, Ont. (2); NMC58-199: Rideau River, Ont. (1); NMC60-262: St. Cedars Rapids, P.Q. (3); NMC58-297, Long Sault Rapids, Ont. (3); NMC60-250: Verdun, P.Q. (1); NMC58-7: Ottawa, Ont. (1); NMC58-223: Georgian Bay, Ont. (1); NMC60-251: Rivière des Prairies, P.Q. (1); NMC63-221: Deer River, Richmond Gulf, P.Q. (2); NMC60-495-A: 14 miles S of Tobermory, Ont. (10); NMC61-248: Croche Lake, P.Q. (1); NMC60-466-A: Long Point, Ont. (3); NMC60-502-A: 2 miles W of Collingwood, Ont. (11); NMC60-513-A: 2½ miles E of Owen Sound, Ont. (11); NMC60-501-A: 9 miles W of Collingwood, Ont. (1); NMC61-294: Bear Island, Ont. (1); NMC60-536-A: Grafton, Ont. (1); NMC61-243: Lake St. Joseph, Ont. (1). *Cottus cognatus*: NMC-58-358: Ft. Chimo, P.Q. (11); NMC59-379: Ft. Chimo, P.Q. (6); NMC60-270: Port Neuf Co., P.Q. (6); NMC60-255: Raymond, P.Q. (6); NMC60-254: 22 miles W of Quebec, P.Q. (6); NMC60-269: Pont Rouge, P.Q. (6); NMC60-138: Quebec, P.Q. (1); NMC60-147:Pickering Township, Ont. Co., Ont. (10); NMC59-401: Koksoak River, P.Q. (4); NMC58-352: Ft. McKenzie, P.Q. (2); NMC60-272: Pont Rouge, P.Q. (4); NMC63-221: Deer River, Richmond Gulf, P.Q. (7).

J. FISH. RES. BD. CANADA, **21**(5), 1964.
Printed in Canada.

TABLE I. Comparison of diagnostic characters in *Cottus bairdii* and *C. cognatus*.

Species	Number of dorsal rays[a]					Number of anal rays[a]							Number of pelvic rays[b]		Number of pectoral rays[b]						Last rays of dorsal		Last rays of anal	
	15	16	17	18	19	10	11	12	13	14	15	16	3	4	12	13	14	15	16	17	Double	Single	Double	Single
bairdii	0	3	11	27	19	0	0	4	13	26	16	1	1	59	0	3	19	35	2	1	58	2	60	0
cognatus	1	23	33	12	1	2	25	31	11	1	0	0	63	7	2	31	32	5	0	0	5	65	18	52
	79% separation					88% separation							94% separation		79% separation						95% separation		86% separation	

Species	Total number pelvic + pectoral + anal[a] + dorsal rays[a]													Total number pelvic + pectoral + anal rays[a]									Number of postmaxillary pores[b]	
	42	43	44	45	46	47	48	49	50	51	52	53	54	26	27	28	29	30	31	32	33	34	35	One	Two
bairdii	0	0	0	0	0	4	4	6	8	19	12	5	2	0	0	0	0	6	6	14	20	11	3	47	13
cognatus	3	4	16	14	20	12	0	0	1	0	0	0	0	2	11	23	24	8	1	1	0	0	0	19	51
	96% separatiou													94% separation									74% separation	

Species	Length of longest ray of anal fin : standard length													Palatine teeth[b]		Caudal peduncle length : Postorbital[c] distance	
	.09	.10	.11	.12	.13	.14	.15	.16	.17	.18	.19	.20	.21	Present	Absent	Less than	More than
bairdii	3	0	8	14	17	13	3	2	0	0	0	0	0	57	3	60	0
cognatus	0	0	1	2	10	9	14	12	11	10	0	0	1	5	65	0	70
	79% separation													94% separation		100% separation	

[a]Each of last two dorsal and anal rays counted even if close, basally.
[b]Determined on left side.
[c]Measured from eye to bony edge of operculum.

In Table I, a comparison is given of the effectiveness of 12 diagnostic characters in separating the two species. The percentage of specimens separable by each character was calculated; chi square tests indicated that the probability that the differences were due to chance was less than 0.005 in each case.

The only character that permitted 100% separation was the ratio of caudal peduncle length to postorbital distance. In *bairdii* specimens the caudal peduncle length was always less than the postorbital distance, in *cognatus* always more.

The last two dorsal and anal rays were sometimes closely approximated at the base. In counting anal rays, a higher degree of separation (88%) was achieved if the last two elements were counted separately than if they were counted as one when close together at the base (78%). In *bairdii* the last two rays of the dorsal and anal fins were more frequently doubled on the last basal than in *cognatus*. The greater anal ray length in *cognatus* results in these rays being incised (compare in Fig. 2). Males of both species tended to have longer rays. In *bairdii* males usually had anal rays .13 to .14 of standard length, females .11 to .13; in *cognatus* the males usually had .15 to .18, the females .13 to .15.

Some other characters, not analyzed in the Table, may be mentioned. Color characters noted by Hubbs and Lagler (1949) in Isle Royale specimens usually held for specimens in the present study. Further, in *bairdii* the dark

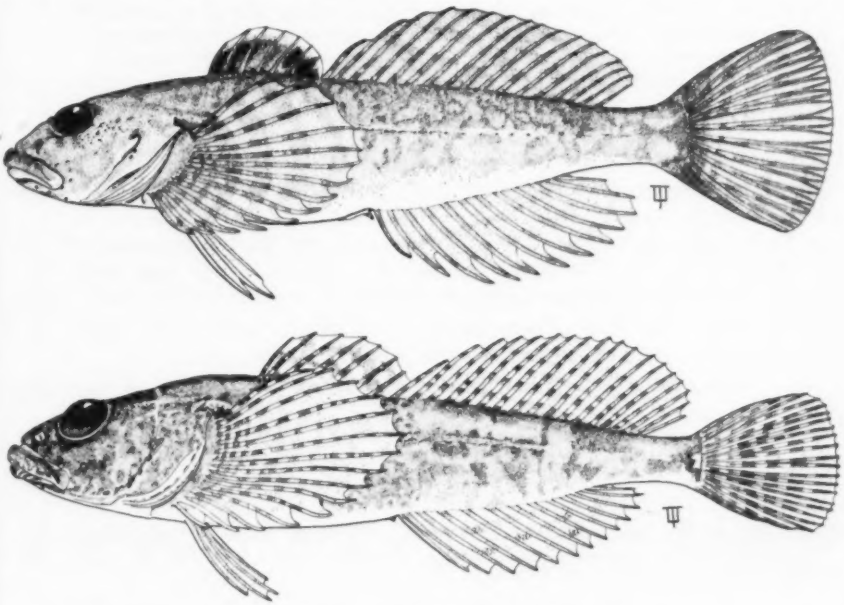


FIG. 2. *Cottus cognatus* above, and *Cottus bairdii* below. Note the longer caudal peduncle and anal rays and the obviously more incised anal rays in *cognatus* (*cognatus* ♂ 84 mm s.l., Raymond Station, P.Q.; *bairdii* ♂ 67 mm, Sawmill Creek, Ottawa, Ont.).

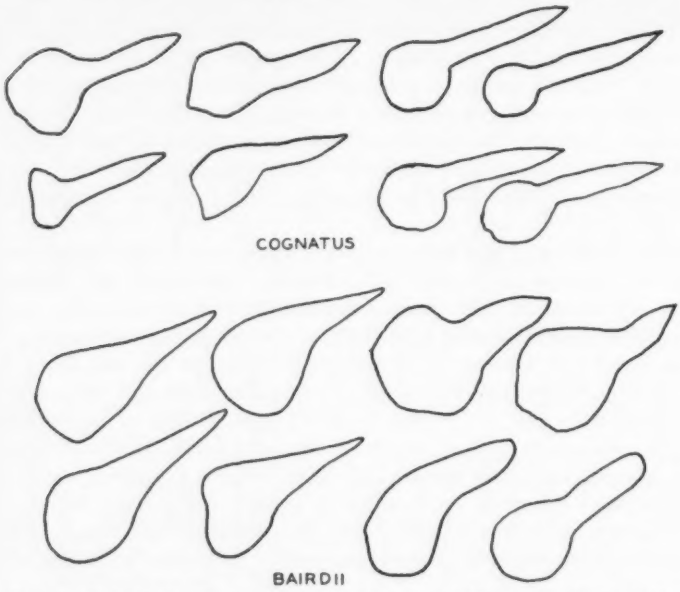


FIG. 3. Prickles in *Cottus cognatus* and *Cottus bairdii* showing intraspecific and interspecific variation in form. Prickle shafts in *cognatus* are longer and more slender, the base smaller, the base being smaller than the shaft length in *cognatus* but nearly equal to it in *bairdii*. (Upper left NMC60-269, P.Q.; upper right NMC60-169, B.C.; lower left NMC60-262, P.Q.; lower right NMC59-40, Ont.).

bands on the pectoral fin were narrow and did not exceed the pupil diameter, while in *cognatus* the pectoral bands were broader and the widest band(s) exceeded the diameter of the pupil (Fig. 2).

The prickle shafts tended to be stouter in *bairdii* than in *cognatus*, and the base larger (Fig. 3). The prickles of British Columbia *bairdii* specimens (previously called *hubbsi*) had even larger bases (see figure 3, McAllister and Lindsey, 1961).

The mouth and head of *bairdii* tend to be larger.

National Museum of Canada
Ottawa, Ontario

D. E. MCALLISTER

Received for publication March 23, 1964.

REFERENCES

BAILEY, REEVE M., AND CARL E. BOND. 1963. Four new species of freshwater sculpins, genus *Cottus*, from western North America. *Occasional Papers Mus. Zool, Univ. Michigan*, No. 634, pp. 1–27.

HUBBS, CARL L., AND K. F. LAGLER. 1949. Fishes of Isle Royale, Lake Superior, Michigan. *Papers Michigan Acad. Sci.*, **33**: 73–133.

MCALLISTER, D. E., AND C. C. LINDSEY. 1961. Systematics of the freshwater sculpins (*Cottus*) of British Columbia. *Bull. Nat. Mus. Canada*, No. 172, pp. 66–89.

RECENT ARTICLES ON INVESTIGATIONS OF THE FISHERIES RESEARCH BOARD OF CANADA PUBLISHED IN OTHER PERIODICALS

Studies No.

861. **Ackman, R. G., and P. M. Jangaard.** 1963. Identification of the major polyunsaturated C_{16} acids of marine oils by GLC separation factors on normal and organosilicone polyesters. J. Am. Oil Chemists' Soc., **40**(12). 744–745.

862. **Vernon, E. H., A. S. Hourston and G. A. Holland.** 1964. The migration and exploitation of pink salmon runs in and adjacent to the Fraser River Convention Area in 1959. Intern. North Pacific Fisheries Comm., Bull. No. 15.

863. **Kennedy, W. A.** 1964. The great lakes of the world (Chairman's introductory remarks). Verh. Internat. Verein. Limnol., **15**: 57–58.

864. **Brockerhoff, H., R. J. Hoyle and K. Ronald.** 1964. Retention of the fatty acid distribution pattern of a dietary triglyceride in animals. J. Biol. Chem., **239**(3): 735–739.

865. **Drummond, G. I., M. W. Gilgan, E. J. Reiner and Michael Smith.** 1964. Deoxyribonucleoside-3′,5′ cyclic phosphates. Synthesis and acid-catalysed and enzymic hydrolysis. J. Am. Chem. Soc., **86**: 1626–1630.

866. **MacLeod, Robert A., R. E. E. Jonas and E. Roberts.** 1963. Glycolytic enzymes in the tissues of a salmonoid fish (*Salmo gairdnerii gairdnerii*). Canadian J. Biochem. Physiol., **41**: 1971–1981.

867. **Dyer, W. J.** 1964. Basic quality changes in frozen seafood. American Society of Heating, Refrigeration and Air-conditioning Engineers, Inc. (ASHRAE), **6**(5): 40–42.

868. **Saunders, J. W., and M. W. Smith.** 1964. Planting brook trout (*Salvelinus fontinalis* [Mitchill]) in estuarial waters. Canadian Fish Culturist, No. 32, pp. 25–30.

869. **Margolis, L.** 1964. *Paurorhynchus hiodontis* Dickerman, 1954 (Trematoda: Bucephalidae): a second record involving a new host and locality in Canada. Canadian J. Zool., **42**(4): 716.

870. **Yablokov, A. V., and D. E. Sergeant.** 1963. [Cranial variation in the harp seal (*Pagophilus groenlandicus* Erxleben, 1777).] Zoologicheskiĭ Zhurnal, **42**(12): 1857–1865. [FRB Translation No. 485.]

871. **Antia, N. J., and C. Y. Lee.** 1964. The determination of "free" amino sugars in seawater. Limnol. Oceanogr., **9**(2): 261–262.

872. **Ross, Herbert H., and William E. Ricker.** 1964. New species of winter stoneflies, genus *Allocapnia* (Plecoptera, Capniidae). Trans. Illinois State Acad. Sci., **57**(2): 88–93.

Copies of individual reprints, if available, may be obtained from the authors or Board establishments through which the investigations were conducted.

Reprints of these articles are included in an annual volume of "Studies", composed of two parts. These are distributed to a selected mailing list. (Articles numbered 776 to 817 appeared in the Studies for 1963, Part 1.)